THE SOUTH AMERICAN SPECIES OF *OENOTHERA* SECT. *OENOTHERA* (*RAIMANNIA*, *RENNERIA*; ONAGRACEAE)[1, 2]

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Abstract

This paper provides an account of the native and naturalized South American species of *Oenothera* sect. *Oenothera* (Onagraceae). Included are 63 taxa (species and subspecies) of three subsections, of which 58 are native in South America and the remainder introduced from North America (*Oenothera laciniata* subsp. *laciniata, O. drummondii, O. villosa*) or possibly from Europe (*O. erythrosepala, O. biennis*). Subsection *Munzia* includes 57 taxa, subsect. *Raimannia* 3 (*O. laciniata* subsp. *laciniata, O. laciniata* subsp. *pubescens, O. drummondii*), and subsect. *Euoenothera* also 3 (*O. erythrosepala, O. villosa, O. biennis*).

The main focus of this monograph is a revision of the exclusively South American subsect. *Munzia*, which is divided into the three series *Renneria, Allochroa,* and *Clelandia.* All taxa were cultivated at the Botanical Institute of the University of Düsseldorf from one to

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[1] Dedicated to my wife and my children Nikola, Lorenz, Bernadette, Gabriel and Christoph.

[2] I would like to thank those who have made the completion of this study possible. Prof. Wilfried Stubbe not only allowed me to work on this problem but also most generously provided facilities in the Botanisches Institut at the University of Düsseldorf. Prof. Peter H. Raven made it possible for me to study for six months at the Missouri Botanical Garden, during which time I was also able to visit South America for two months. My work in St. Louis and in South America was supported by a grant from the U.S. National Science Foundation to Dr. Raven, who also translated this manuscript from German. His interest and cooperation were invaluable for my work, and useful discussions concerning it were also held with Prof. Stubbe, Dr. A. Basler, Dr. M. Drillisch, and Dr. H. Kutzelnigg.

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Material from the following herbaria was examined, and I am grateful to those who made the material in their charge available for study: AAU, AI (by Raven), AK, AMD, B, BA, BAA, BAB, BAS, BB, BM, BR, BREM, C, COI, CONC, CORD, CTES, DUSS, E, F, FR, G, GH, GOET, HB, HBG, HBR, K, L, LD, LE, LIL, LISE, LISU, LP, LY, M, MEL, MICH, MO, MPU, MVFA, ND, NSW, NY, P, PERTH, POM, PR, PRC, PRE, R, RAW (by Raven), RB, RSA, S, SGO, SI, SP, SRGH, UC, UPS, US, USM, W, Z, and the private Herbarium of Dr. A. Ruiz Leal, Godoy Cruz, Mendoza, Argentina (Leal).

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several wild strains. Cytological examination of meiosis in 600 plants representing 280 strains showed that 20 taxa were chromosomally homozygous, forming 7 bivalents at meiotic metaphase I. All other taxa were complex heterozygotes forming a ring of 14 chromosomes at meiotic metaphase I or with a smaller but still stable ring configuration (ring of 12 and 1 bivalent, ring of 8 and ring of 6, or ring of 10 and ring of 4). Homozygous species were distributed throughout the range of subsect. *Munzia*. Some of the individual chromosomally homozygous species also had individual wide ranges; for example, *O. scabra* and *O. versicolor* (series *Renneria*), *O. mendocinensis*, *O. odorata*, *O. indecora*, *O. affinis*, and *O. ravenii* (series *Allochroa*).

The following species of subsect. *Munzia* were adventive or established outside of South America: (1) *O. mendocinensis*: Europe (adventive); (2) *O. longiflora* subsp. *longiflora*: Europe, Atlantic Islands (Azores, Madeira, Canary Islands, Cape Verde Islands), South Africa, Australia; (3) *O. indecora* subsp. *indecora*: Europe (adventive); (4) *O. indecora* subsp. *bonariensis*: Europe (adventive), Australia, South Africa, Tristan da Cunha (adventive?); (5) *O. affinis*: Europe, India, Pakistan, Australia, Hawaii, South Africa; (6) *O. mollissima*: U.S.A. (adventive?), Australia; (7) *O. stricta* subsp. *stricta*: U.S.A., Mexico, Hawaii, Europe, Japan, India, Pakistan, Sri Lanka, Java, Australia, New Zealand, North Africa, South Africa, Ethiopia; (8) *O. parodiana* subsp. *parodiana*: South Africa, Europe (adventive).

The common ancestor of *Oenothera* sect. *Oenothera* subsect. *Munzia* seems to have arrived in South America from North America no more than a few million years ago, and to have given rise to some 57 taxa there subsequently in response to drastic climatic changes and increasing elevation of the mountains in that continent. *Oenothera laciniata* subsp. *pubescens* seems to have arrived in South America from North America much more recently, perhaps within the past 100,000 years.

Oenothera has been the subject of genetic and evolutionary investigations for a very long time, owing mainly to its unusual genetic system, which involves complex heterozygosity. The species of the so-called "*Euoenothera*" group of North America have been intensively studied for more than 70 years (summary, Cleland, 1972), but other members of the genus have not been considered in such depth. In Düsseldorf, a program has been conducted for more than 15 years on the biosystematics of the South American species of *Renneria* (Fischer, 1962) and *Raimannia* (Munz, 1935). In this work an extraordinarily rich array of wild populations of the group assembled under the direction of Professor Doctor Wilfried Stubbe has been utilized. The object has in part been to work out a more satisfactory taxonomic rearrangement of the South American species of these two closely related groups. Extensive investigations of the genetics of both groups had been carried out earlier by Professor J. Schwemmle of Erlangen and his students, but the results have not, for the most part, been applied to the systematics of these taxa.

Hybridization has played an important role in the evolution of many groups of the genus *Oenothera*, so that a satisfactory taxonomy often can be worked out only on an experimental basis. In the course of my investigations with hundreds of strains of living plants at the University of Düsseldorf, I was able to ascertain that the most recent revision of subgenus *Raimannia* (Munz, 1935) was inadequate in dealing with the rich pattern of variation in this group. It was soon evident that there were many more distinct entities than had previously been thought to exist; the phenomenon of complex heterozygosity had not been taken into account in earlier efforts to classify the subgenus. In the case of *Renneria*, no revision of the entire group has hitherto been available. In the more recent floristic and taxonomic literature all species have been treated under the names *Oenothera campylocalyx* and *O. rubida*.

The common ancestor of what have been regarded as the subgenera *Euoenothera*, *Raimannia*, and *Renneria* of *Oenothera* almost certainly originated in the semiarid to subhumid regions of western North America in mid-Tertiary time (Raven, pers. comm.). This region is, in fact, the center of evolution of the entire tribe Onagreae, to which *Oenothera* belongs. Geologically speaking, the arrival of *Oenothera* in South America seems to have been very recent, an event of the past several million years (Raven & Axelrod, 1974). Aside from five of the ten species of *Hartmannia* (Raven & Parnell, 1977) and two of *Lavauxia*, all indigenous South American species of *Oenothera* are included in sect. *Oenothera* and are treated in this revision.

Considering the reticulate relationships between the species grouped by Munz (1965) as the subgenera *Oenothera* and *Raimannia*, as well as the complex pattern of relationships among the South American species of this group, it seems preferable to regard all as belonging to a single infrageneric taxon. This taxon is well differentiated from all other groups in the genus, both morphologically and in terms of its crossability. In accordance with the practice established for all other genera of Onagraceae, this group is designated a section, sect. *Oenothera*. The South American species of this section, all but four of which are assigned to the newly described, endemic subsection *Munzia*, are the subject of this revision.

Oenothera sect. *Oenothera* subsect. *Munzia* is regarded as comprising three series and 45 species, of which three are divided into two subspecies each and five others are divided into three subspecies each, for a total of 57 taxa. One or more strains of each of these were cultivated in the experimental garden at the Botanical Institute of the University of Düsseldorf. All plants examined cytologically were diploid, $2n = 14$. The cytological examination of 600 plants representing 280 strains showed that 20 species formed pairs of chromosomes at meiotic metaphase I. All others were complex heterozygotes that formed either a complete ring of 14 chromosomes at meiotic metaphase I or a stable ring configuration (ring of 12 and 1 bivalent; ring of 8 and ring of 6, or ring of 10 and ring of 4).

Many of the species of subsect. *Munzia* vary in such a way that they could be subdivided into several more species if the pattern of distribution of their morphological characteristics were taken as preeminent. In other words, if all of the small differences within the subsection that are preserved by the syndrome of self-pollination and complex heterozygosity, and which have in many cases come to characterize populations, were to be recognized taxonomically, one could recognize literally hundreds of species without any gain whatsoever in taxonomic utility.

There are many direct genetic connections between the South American species recently referred to subg. *Renneria* (Fischer, 1962) or earlier to subg. *Euoenothera* (Munz, 1933) and those referred to subg. *Raimannia* (Munz, 1935). The South American species referred to these two groups are completely interfertile with one another. Judging by the patterns observed, hybridization seems often to have occurred in nature, and at least a dozen species, referred in this monograph to series *Clelandia*, seem to have originated as complex heterozygotes between these two morphologically quite distinctive groups. The species assigned to this series combine one genome derived from series *Renneria* with another derived from series *Allochroa*. The group is not, however, to be regarded as a transitional one between these two series; no such transition exists. Rather it has originated as a result of hybridization between individual species of *Renneria* and individual species of *Allochroa*, as a result of which the species share a number of characteristics in common. The differentiation of the narrow-fruited ancestors of series *Allochroa* took place first, evidently from plants that resembled those now assigned to series *Renneria*. Presumably this took place at the southern end of the area of distribution of series *Renneria*, which is the region of overlap between the two series at the present time (Fig. 7), and therefore the area in which the species of series *Clelandia* are concentrated. It appears likely that many of the species of this series might have had a very recent origin; with the exception of *O. magellanica* and *O. punae*, each has a restricted area of distribution.

Genetic relationships thus seem to demonstrate a unity between South American species of *Raimannia* and the group that has recently been called *Renneria*. On the other hand, the North American species of *Raimannia*, including *O. laciniata*, do not appear to be closely related to any species of this South American group as its members are to one another, and they are here regarded as comprising a separate subsection *Raimannia*. This group is native only in North America with the exception of the entity that has been called *O. laciniata* subsp. *pubescens*, which ranges south to Colombia, Ecuador, and Peru.

To series *Renneria* (13 species) belong all species with short, urn-shaped capsules, except for one element within the species *Oenothera nana* which was put in sect. *Raimannia* by Munz (1935); see p. 488. Series *Allochroa* (21 species) comprises only a portion of the South American species of *Raimannia*, for which a new name was needed since *O. laciniata* is the type of *Raimannia*. Since the complex connections between *Renneria* and *Allochroa* are now better understood, species of hybrid origin between them, all complex heterozygotes, have been designated as a distinct series here named *Clelandia* (11 species). The species here treated as series *Clelandia* have generally been treated in the literature under the names *O. odorata*, *O. stricta*, *O. indecora*, and *O. nana*.

The species of *Renneria* (in the sense of Fischer, 1962), with their subangular seeds and heavyset capsules, are confined to the high Andes. They probably are close to the ancestral form for the section, and may have subsequently given rise to the other South American groups. The species of series *Allochroa* occur mainly at lower elevations, although some species do extend into the moun-

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FIGURES 1–4. Habitats of *Oenothera* sect. *Oenothera* taxa in South America.—1. Habitat of *O. nana* and *O. punae*, between Yaví and La Quiaca, 3,500 m, Jujuy, Argentina (Santarius).—2. Habitat of *O. indecora* subsp. *bonariensis*, Itajaí, Santa Catarina, Brazil (Dietrich).—3. Habitat of *O. catharinensis*, Isle of Santa Catarina, Santa Catarina, Brazil (Dietrich).—4. Habitat of *O. stricta* subsp. *stricta* and *O. villaricae*, Río San Pedro near Lago Riñihue, Valdívia, Chile (Stubbe).

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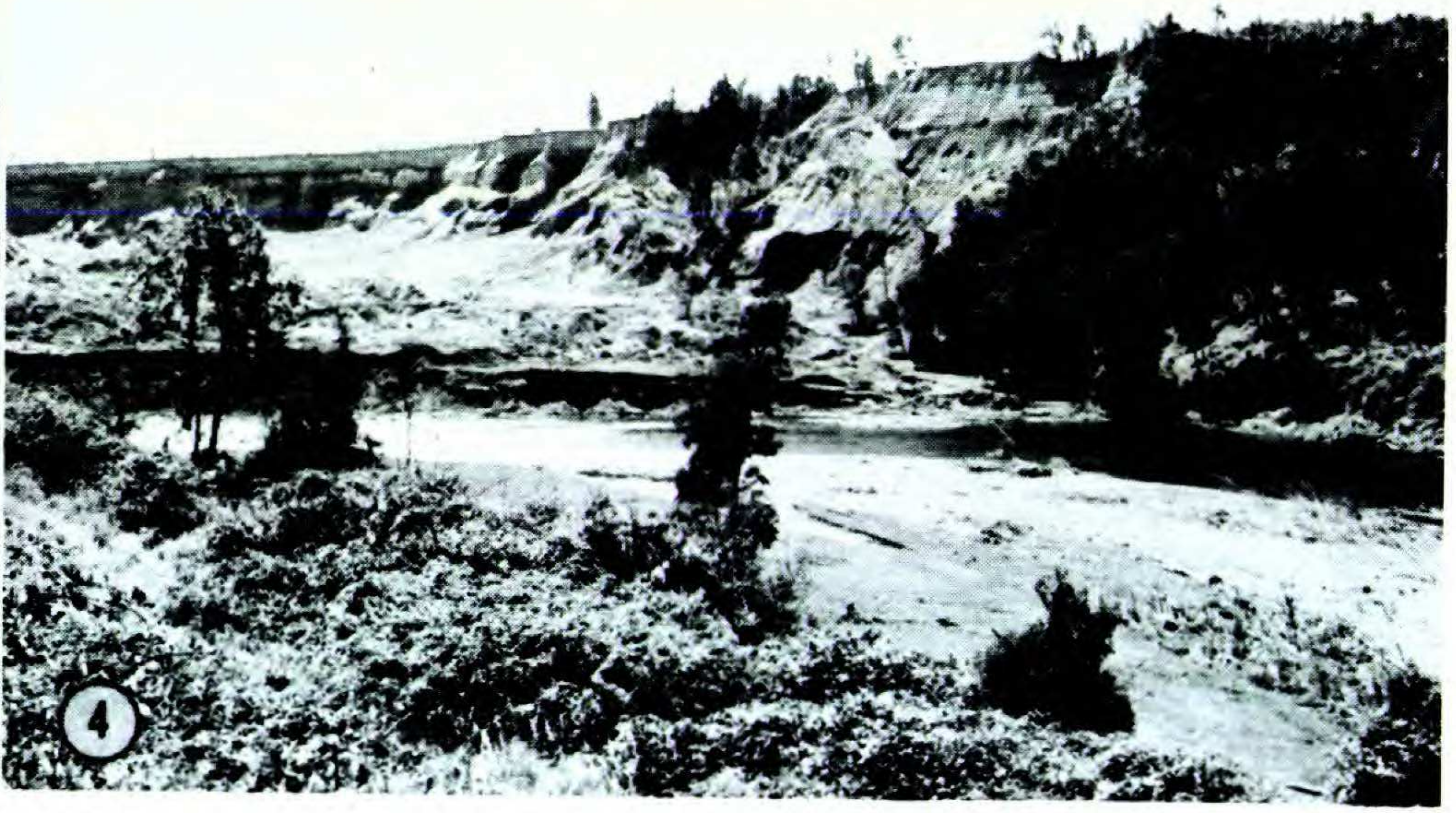

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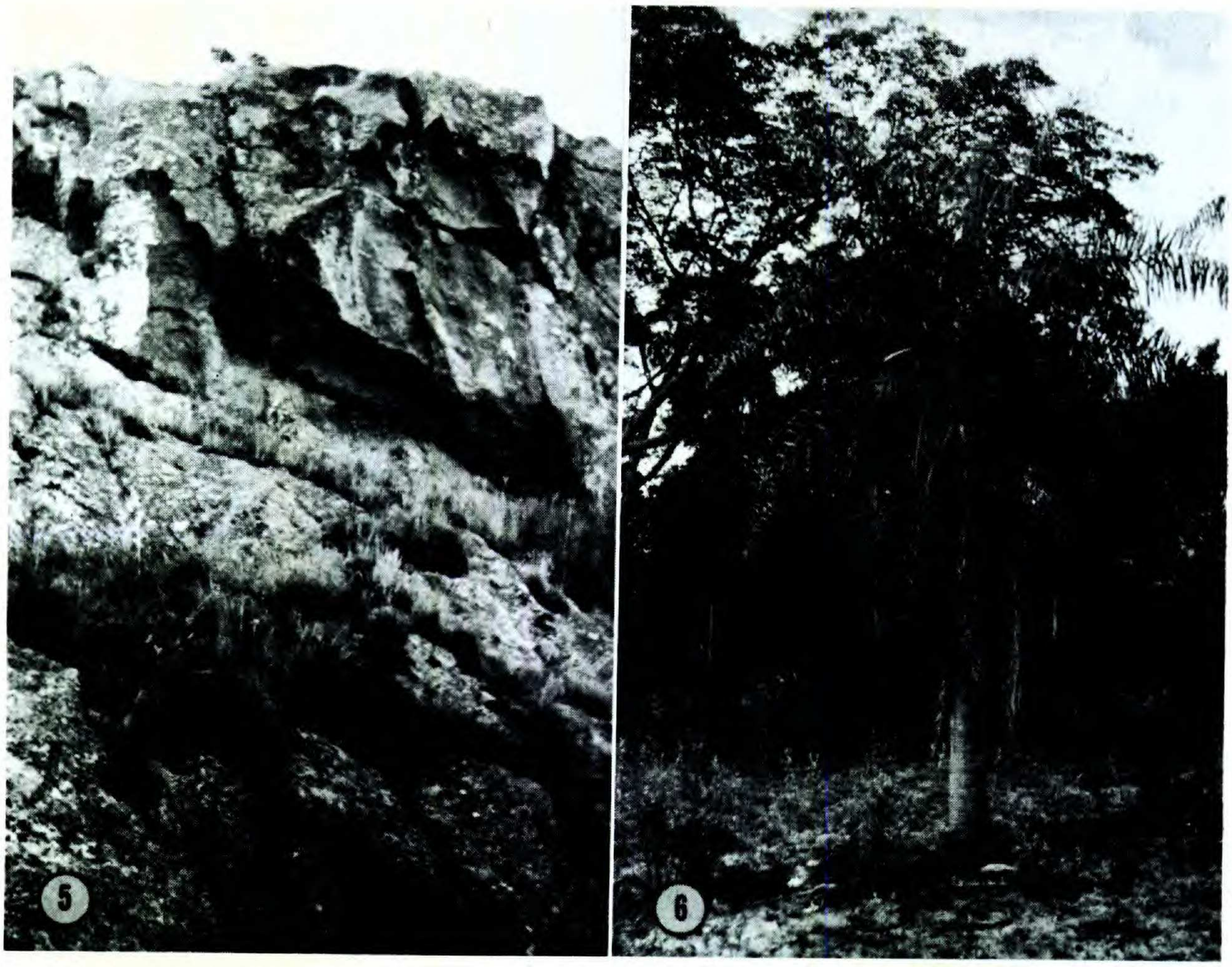
tains. In the South American continent, various lines of the section have radiated into habitats ranging from coastal beaches to relatively high elevations. The common ancestor of these groups seems to have reached South America within the past several million years (Raven & Axelrod, 1974). It radiated extensively in South America in relation to the many drastic changes in habitats that occurred in the Pleistocene and more recently (Simpson, 1975). The arrival of *O. laciniata* subsp. *pubescens* in South America was probably an event that occurred considerably later, perhaps only 100,000 years or so ago.

Cytogenetic Basis of Evolution

Just as in North American species of subsect. *Euoenothera*, there occur among the South American members of sect. *Oenothera* species which are chromosomally homozygous and form pairs of chromosomes or small rings at meiotic metaphase I, as well as others which are complex heterozygotes and form a ring of 14 or other large rings at meiotic metaphase I. Some of the plants which are essentially chromosomally homozygous also form small rings which segregate in an alternate fashion at meiotic metaphase I. All of the complex heterozygotes are highly self-pollinating as they are throughout the Onagraceae, with the possible exception of *O. erythrosepala*, whereas the chromosomal homozygotes range from self-pollinating to strongly outcrossing. All homozygotes of subsect. *Munzia* that have been investigated were genetically self-compatible. Most of the complex heterozygote species are true-breeding hybrids which combine genomes from two species which may be very distinct from one another. Their progenies are however uniform; they behave as true-breeding distinct species in nature. On account of the alternate disjunction of the ring of 14 chromosomes in such complex heterozygotes, two sets of 7 chromosomes behave as two different chromosomes when segregating in meiotic anaphase I. In this way the possibility of interchange between the two genomes and consequent segregation is minimized.

Additional aspects of the genetic system, such as lethal factors, genes for self-sterility, and selective fertilization (Arnold, 1962; Schwemmle, 1968) prevent the reconstitution of the homozygotes at least in a viable form. Following self-fertilization, which is the rule in the complex heterozygotes, or outcrossing with another similar individual of the same population, the complex heterozygote is always reconstituted. Only in exceptional cases does one of the chromosomally homozygous parental types segregate in the progeny of a complex heterozygote, as discussed under *O. acuticarpa* on p. 606.

Cleland (1972: chap. 7) has given a plausible explanation for the origin of the rings of 14 chromosomes which occur in complex heterozygotes of *Oenothera*. The rings are formed because of reciprocal translocations between nonhomologous chromosome arms. Such reciprocal translocations, which probably occur at a low frequency in all groups of organisms but become a regular part of the adaptive system in only a few, do not lead to an unequal distribution of the chromosomes to the poles in *Oenothera* because of regular alternate disjunction of rings of chromosomes in this genus. All of the chromosomes are the same length, have



FIGURES 5–6. Habitats of *Oenothera* sect. *Oenothera* taxa in South America (continued). —5. Habitat of *O. santarii*, Cerro los Gigantes, 2,000 m, Sierra Grande, Córdoba, Argentina (Dietrich).—6. Habitat of *O. ravenii* subsp. *ravenii*, San Bernardino, Lake Ypacaraí, Cordillera, Paraguay (Dietrich).

arms of equal length, and appear euchromatic only at the end segments; this structure may facilitate alternate disjunction in the rings (Kurabayashi et al., 1962). Similar translocations between dissimilar nonhomologous chromosomes would lead to a high percentage of misdivision and therefore to a degree of sterility in the plants in which they occurred.

In the evolution of the genus *Oenothera* the phenomenon of reciprocal translocation has played a decisive role. Following self-pollination or crossing of plants with small rings of chromosomes, it is possible to observe in the progeny not only chromosomal homozygotes which form 7 bivalents structurally identical to the original form of the species but also others which differ from the original form in the arrangement of their chromosome arms. Such plants constitute the starting point for the origin of new complex heterozygote species in the genus *Oenothera*. Through the hybridization of homozygous strains with others with a sufficiently different end arrangement, a ring of 14 or other stable configuration may arise, and then we can speak of permanent structural heterozygosity.

In contrast to the North American species of subsect. *Euoenothera*, there are among the South American species many homozygous ones in addition to a rich array of complex heterozygotes. Since all complex heterozygotes are by definition capable of being traced back to a homozygous original form, we have attempted in the course of our work to synthesize existing complex heterozygotes through hybridization between existing chromosomally homozygous species when possible, and by crossing such complex heterozygotes back to their putative parents to illuminate the nature of the chromosomal complexes contained in them.

It was possible to make a very comprehensive analysis of the complex heterozygotes in this group owing to the virtually unrestricted crossability of all species of this section. Fortunately, all of the genomes represented in the complex heterozygotes among the South American species are still represented in homozygous combinations among other species of the group. This should not be taken to infer that the phenotypes of these homozygous species are absolutely identical with those of the strains which originally gave rise to the complex heterozygotes, however, for many genomes have during the time they were combined in such complex structural heterozygotes become altered to a certain degree.

Although *Oenothera* does have an unusual genetic system, hybridization may play no greater a role in the origin of new species in this genus than it does in many groups of higher plants (e.g., Ehrendorfer, 1971). Only in the exact method of origin of the complex heterozygotes, which may perpetuate intermediate hybrid phenotypes, do they differ strikingly from methods of the origin of species through hybridization found in other groups of plants.

Distribution and Phylogenetic Relationships

The general range of the South American species of this group and of the individual series is shown in Fig. 7. Especially notable is the extensive zone of overlap between *Renneria* and *Allochroa* as well as the frequency of chromosomally homozygous species of both subsections in the vicinity of the Cordillera Oriental of Argentina. In addition, most species of the entirely hybrid series *Clelandia* occur in this area. The occurrence of so many species of both groups, and of the intermediates between them, in this particular region is probably related to the very close genetic relationship between *Allochroa* and *Renneria*, plants similar to the latter group having probably given rise to the original members of series *Allochroa* during the past.

Rapid evolution of the species of the two groups in this region has no doubt been made possible in part by the rich diversity of habitats found in a relatively limited area along the east side of the Andes. Moreover, because of the impenetrable tropical forest and of the Gran Chacó, it is not surprising that the first migration out from the region of the Cordillera Occidental occurred towards the east and southeast into the open plains of Argentina. From here, secondary migration eventually resulted in the colonization of Paraguay, Uruguay, and southern Brazil. Ultimately members of this group migrated by way of the Andean passes to Chile.

Species of series *Renneria* occur outside of the Andes only in the highest elevations of the Sierra Grande and the Sierra de Comechingones. Only their derivatives in which the characteristic phenotype of series *Allochroa* was evolved

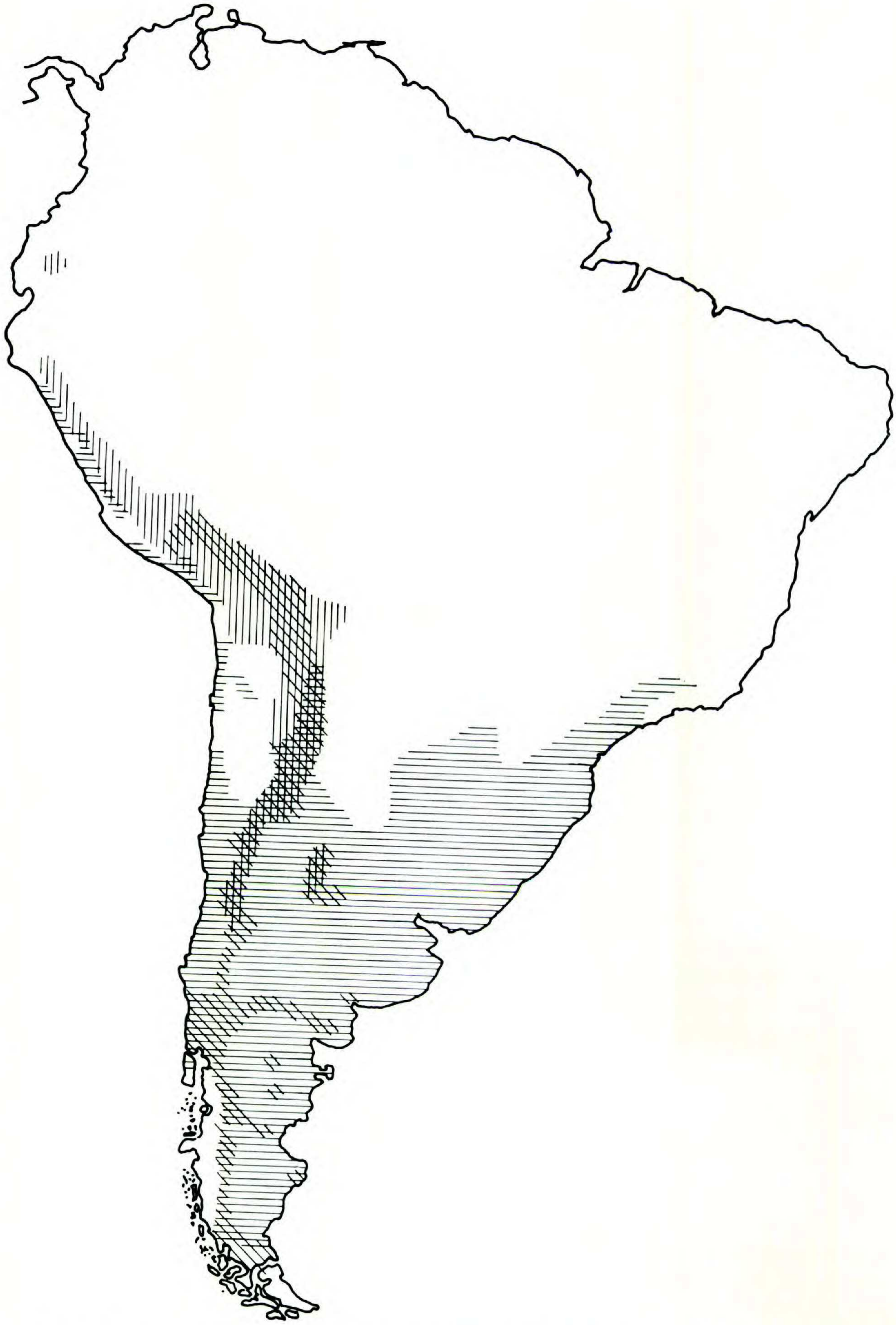


FIGURE 7. Areas of the three series of subsect. *Munzia*: ser. *Renneria*, vertical lines; ser. *Allochroa*, horizontal lines; ser. *Clelandia*, diagonal lines.

were able to colonize the plains and eventually reach the seacoast. The species of series *Renneria* have remained strictly adapted to the high mountains.

In Fig. 7 it can also be observed that the combination of genomes from series *Renneria* with those from series *Allochroa*, resulting in the origin of the entirely complex heterozygotes of series *Clelandia* resulted in plants which were able to greatly extend the area of the two parental series. On the one hand, series *Renneria* was able to penetrate to the southernmost point of the continent of South America at Punta Arenas only in the combination *Oenothera magellanica*, while on the other hand series *Allochroa* was able to penetrate to high elevations in the mountains of southern Peru only in the combination known as *O. punae*.

Figure 8 is a plausible phylogenetic scheme for the evolution of series *Allochroa* from *Renneria*. *Oenothera odorata* and *O. mendocinensis* were derived from a plant which probably resembled the present day *O. santarii*, and they have remained confined mainly to the southern regions of South America. On the other hand, *O. ravenii*, *O. longiflora*, *O. indecora*, and *O. affinis* have extended their ranges mainly to the east. *Oenothera ravenii* and *O. longiflora* may have belonged to a group which developed around plants with a phenotype somewhat like that of *O. longituba*; *O. indecora* and *O. affinis* seem to be more closely related to a plant with the phenotype of *O. scabra*. *Oenothera catharinensis* seems to have been derived from *O. ravenii* as an obligate annual of local distribution. *Oenothera verrucosa* with *O. coquimbensis* and *O. featherstonei* seem clearly to have been derived earlier from plants similar to those of series *Renneria*, and independently from those species mentioned above of series *Allochroa*.

Even though Munz (1935) put the taxa here regarded as series *Allochroa* and *Raimannia* into the same subgenus, it is difficult to establish any direct connection between them. On the other hand, there is a close and demonstrable relationship between the species of *Allochroa* and those of *Renneria*, treated by Munz (1935) as comprising separate subgenera. Their relationship is demonstrated by the fertility of almost any hybrid combination and even more strongly by the compatibility of their plastids. The hybrids between *Renneria* and *O. indecora*, *O. mendocinensis*, and *O. odorata* suggest that these species may be closest to *Renneria*, since they are capable of becoming fully green in both directions. In addition, albino or variegated plants have not been observed to occur among hybrid progenies involving these species with one another. In contrast, there are significant differences between the plastids of subsect. *Raimannia* and those of subsect. *Munzia*: hybrids between *O. laciniata* subsp. *pubescens* and species of *Munzia* were albino or very light green and set seed poorly (unpublished; Stubbe, pers. comm.).

There appears to be full plastome compatibility within the taxa of series *Renneria*, since all hybrids I have observed thus far were fully green. The establishment of differentiated plastome types seems to have taken place within subsect. *Munzia* only after the evolution of series *Allochroa* from *Renneria*. According to present information based on hybrids I have examined, it appears that *O. affinis*, *O. longiflora*, and *O. ravenii* each has its own distinctive plastid type.

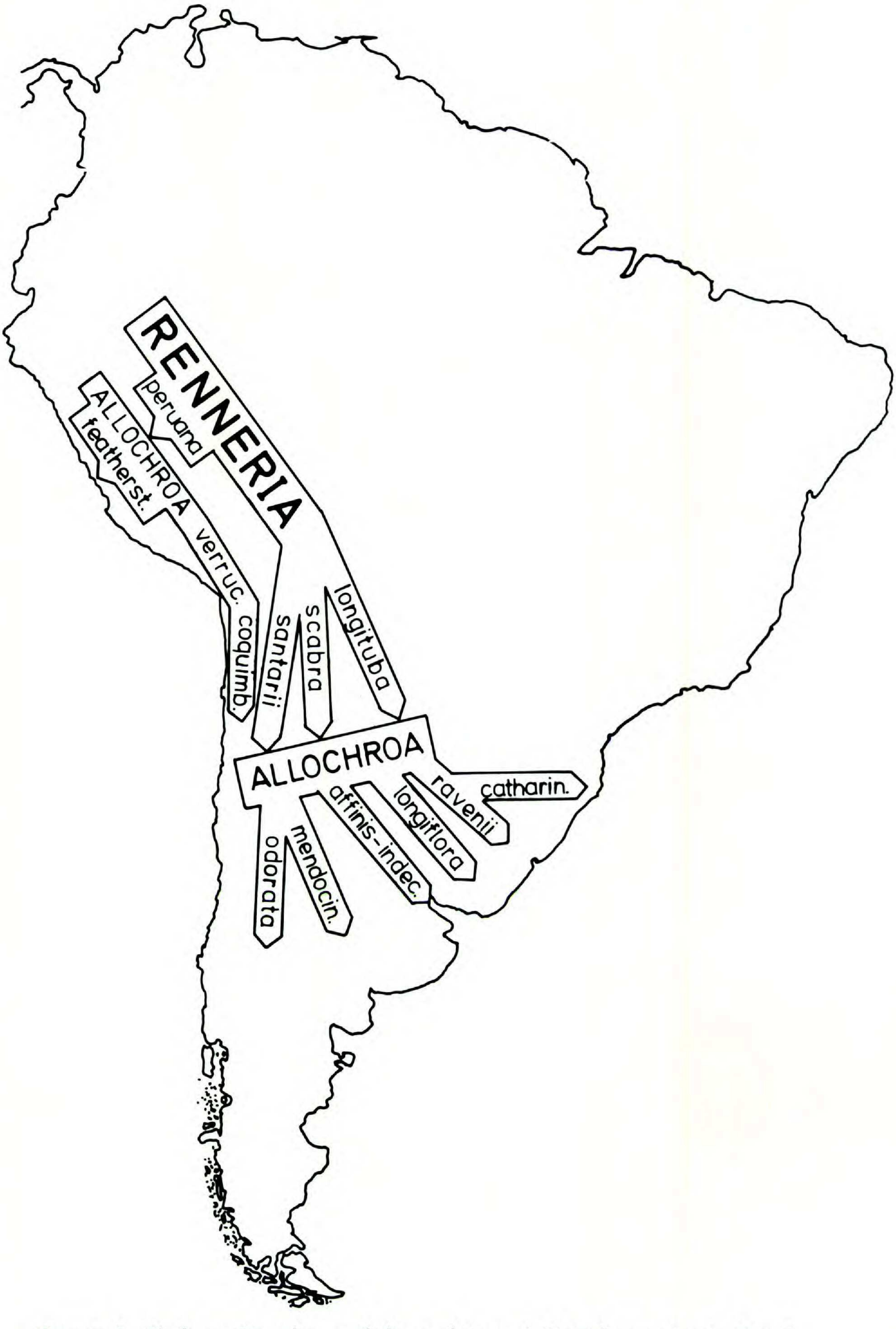


FIGURE 8. Phylogenetic scheme of the evolution of *Oenothera* subsect. *Munzia.*

If this is the case, there would be at least four different plastid types within series *Allochroa*. Our investigations concerning the representation of these four plastid types among the complex heterozygotes are incomplete, and it is not possible to make a definitive statement about this matter at present.

Unlike the situation among the North American species of subsect. *Euoenothera*, distribution of the chromosomally homozygous forms in South America seems to have remained approximately as wide as that of their complex heterozygote derivatives, at least in series *Renneria* and *Allochroa*. Only in the cases of *O. peruana*, *O. santarii*, *O. ravenii*, and *O. longiflora* does it seem likely that the present area of distribution represents only a remnant of an earlier and much wider distribution. In addition, the ranges of *O. verrucosa* and *O. featherstonei* might be regarded as relictual.

Whole series of species of *Renneria* and *Allochroa* seem to have acquired the ability to greatly extend their ranges of distribution, in a sense, by forming new complex structural heterozygous combinations with other species. From this it can be assumed that the ability of these complex heterozygotes to colonize new areas is greater than that of the corresponding homozygotes. This seems to be especially clear with respect to Chile, where only complex heterozygous species of subsects. *Allochroa* and *Clelandia* occur, except, of course, for the occurrence of *O. coquimbensis* in the deserts of the far north.

In the course of their migrations the complex heterozygotes seem often to have migrated by a circuitous path, as can be illustrated especially clearly by the history of the *O. odorata* complex. The *odorata*-complex first of all participated in the origin of *O. stricta*, the other parent being *O. ravenii*. *Oenothera stricta* is now very widespread and abundant in Chile. Figures 241–244 show other examples of the spread of different complexes.

ANALYSIS OF COMPLEXES

The analysis of complex heterozygotes in Düsseldorf was made possible by the comparison of various artificially produced complex heterozygotes with naturally occurring ones. In addition, naturally occurring complex heterozygotes were hybridized with their putative chromosomally homozygous parents in both directions, and the hybrids evaluated morphologically. The association of chromosomes was of no value in most cases in assessing the relative parentage of the different forms. Haustein (1952) pointed out over 20 years ago that chromosomal pairing was of almost no value in determining phylogeny in this group, as it was always complete and variable within many species.

If, for example, a hybrid between a randomly chosen line of *Oenothera versicolor* and one of *O. scabra* formed 7 bivalents, one could certainly conclude that these two strains are related to one another, since the pairing of their chromosomes is undisturbed, and fertility, whether measured by pollen or seeds, is complete. About the degree of relationship between them, however, relative to other species of the group, this test says nothing. In many instances, the evolution of species within series *Renneria* especially seems to have taken place solely by genetic changes, not involving any rearrangement of chromosome structure. As another example, I might mention that "*longiflora* Erlangen," a strain of *O. affinis* (series *Allochroa*), gave a hybrid with a ring of 4 and 5 bivalents when crossed with a strain of *O. scabra* (*Santarius 2003*; series *Renneria*) collected in Bolivia. These structural homologies cannot be taken as a strong indication of a particular relationship between *O. affinis* and *O. scabra*, however, since within *O. affinis* itself, hybrids have been observed to form configurations at meiotic metaphase I ranging from 7 bivalents to a ring of 14.

Other indications that chromosomal configurations in hybrids between various South American species are not a useful index to relationship is provided by the following observations. Even in individual populations of *O. affinis* and *O. odorata*—populations which appear morphologically homogeneous—there may be found individuals forming 7 bivalents, others which form a ring of 14 at meiotic metaphase I, and still others with smaller rings. In short, chromosomal evolution does not seem to have proceeded among this group of species at the same rate as morphological evolution, and the two do not appear to be highly correlated. Variation of this sort has been found in limited areas; for example, *Santarius 1869* represents a sample that in the experimental garden was morphologically indistinguishable from *Santarius 1850*, and both were referable to *O. affinis*. When hybridized, these two populations yielded progeny in which the plants formed a ring of 14 at meiotic metaphase I. On the other hand, when plants from *Santarius 1869* were hybridized with a morphologically very distinctive strain with broad leaves from 1,600 km away—*Santarius 193*—they formed a ring of 4 and 5 bivalents. When they were hybridized with *Santarius 1711*, another strain of *O. affinis* from about 350 km away, they formed a ring of 6 and 4 bivalents.

Oenothera affinis is evidently in a stage of evolution in which the chromosomal homozygotes are more widespread and much better represented than the heterozygotes. The sorts of intermediate chromosomal configurations that occur frequently indicate, however, that a wide variety of different end arrangements occurs in the species. In cultivation, the complex structural heterozygotes breed true and do not "throw off" homozygous derivatives.

This pattern is very different from that worked out by Cleland (summary in Cleland, 1972) for the North American subsect. *Euoenothera*. On the basis of his studies of this group, Cleland worked out a theory whereby the accumulation of reciprocal translocations within a population, accompanied by geographical isolation, would lead eventually to the origin of populations which were essentially chromosomally homozygous but characterized by different end arrangements. If these strains eventually spread and came into contact, complex heterozygotes might originate in a single step by hybridization in the zone of contact. These complex heterozygotes, fixed from their origin, would breed true and would eventually replace the chromosomal homozygotes with which they occurred.

A situation similar to that just described for *O. affinis* can be accepted for *O. odorata*. With respect to its chromosomal configurations, *O. odorata* is extremely variable. Plants with 7 bivalents and all configurations up to and including complex heterozygotes with a ring of 14 occur. From this, it can be concluded not only that a variety of differentiated chromosomally homozygous types occur within the species, but also that the species is still in a state of active evolution chromosomally. It is not clear whether the complex heterozygotes within this species have formed through hybridization between chromosomal homozygotes completely differentiated with respect to their end arrangements, or have accumulated following the formation of rings of chromosomes of intermediate size by further spontaneous reciprocal translocation. In some populations, the balance seems to have shifted definitively toward a preponderance or exclusive representation of chromosomal structural heterozygotes, while in others, chromosomal structural instability seems to be the rule. In the vicinity of Comodoro Rivadavia, Prov. Chubut, the essentially stable configuration of a ring of 12 and 1 bivalent seems to have become predominant.

Results such as those discussed for *O. affinis* and *O. odorata*, lead to a view of the origin of complex heterozygosity quite different from that presented by Cleland and others for subsect. *Euoenothera.* In these South American species, as in some others, chromosomal structural heterozygotes occur together with homozygotes and plants with intermediate configurations in the same populations. There is evidently no direct correlation between the formation of strains or populations that are well differentiated either genetically or phenotypically and the origin of complex heterozygosity, since in these cases the only major difference between the genomes represented in the heterozygotes seems to be that concerning the actual end arrangements represented. It seems unimportant whether the pattern of end arrangements responsible for the ring of 14 arose gradually or in a single step.

Oenothera affinis, like all other South American species of the section, is self-compatible and often self-pollinating, the anthers shedding pollen directly on the stigma at anthesis. Therefore, regardless of how a complex heterozygote originates, it would tend to persist in the population alongside plants with other chromosomal configurations owing to regular self-pollination.

This species exhibits several stages of complex heterozygosity. The first, in which homozygotes still segregate from the heterozygotes, is not known in *O. affinis*, although it does occur in *O. acuticarpa.* In the second stage, the complex structural heterozygotes are plants with large flowers and a long floral tube, indistinguishable from chromosomal homozygotes of the same species. The population of *O. affinis* in Chile is probably nearly or quite dominated by complex heterozygotes. However, only one bit of actual cytological information is available (Stubbe in 1961). Examination of the pollen of plants from four populations from the provinces of Atacama, Coquimbo, and Valparaíso (*Johnston 5860*; *Behn 8468*, *22798*; and *Eyerdam 10040*) revealed from 20–35% empty grains, however. A fifth population, from Aconcagua (*Behn 22802*), had essentially no empty grains, which makes it virtually certain that it was chromosomally homozygous. The origin of complex heterozygosity in the Chilean populations seems to have been very recent, and it may be that the original plants that became established on the west side of the Andes were already heterozygotes.

The third phase in the evolution of complex heterozygosity occurs when all plants are small flowered and self-pollinating, although retaining the long floral tube characteristic of *O. affinis*. Further reduction of flower size would lead eventually to plants with a short floral tube also, as has occurred in the evolution of *O. mollissima* from *O. affinis*. The morphological changes that have occurred in *O. mollissima* have been so extensive that it is best regarded as an independent species at the present time (Hecht, 1950; Hecht & Tandon, 1953). Even though these species often occur in mixed populations, the regular self-pollination of *O. mollissima* seems to constitute an effective and sufficient barrier to interspecific hybridization in nature; hybrids occur only occasionally.

The origin of complex heterozygosity in *O. elongata* (series *Clelandia*), in contrast to the situation discussed in *O. affinis* and *O. odorata*, involved hybridization between two distinct taxa. Other clear-cut examples of this sort of evolutionary process are afforded by the origin of *O. magellanica*, *O. siambonensis*, *O. stricta*, and *O. villaricae*. The strain of *O. elongata* from the province of Catamarca (Diers in 1959) has had a remarkable history, quite apart from the fact that the locality is far from the main area of distribution of the species. In 1960, an individual plant appeared in the progeny of a seed sample from *O. longituba* at the same locality, gathered in the wild. In all probability, this plant was a spontaneous hybrid between *O. longituba* and *O. affinis*, both of which commonly grow together in Catamarca. On self-pollination, however, it bred true, and it has now been maintained in cultivation for 13 years as a complex heterozygote, without showing any tendency to segregate the characteristics of its presumed parents. The original plant gave evidence of plastid incompatibility and probably would not have been vigorous enough to survive in the wild; by a fortunate chance, it was grown in the experimental garden to give clear evidence of the mode in which a particular complex heterozygote could have been formed. Evidently the one-step, efficient formation of this chromosomal arrangement deterred the segregation of the parental species from the start.

Spontaneous hybrids with *O. affinis* also appeared in the progenies of two other collections of *O. longituba*, *Santarius 1736* and *1737*. These had intermediate chromosomal configurations, however, of a ring of 6, a ring of 4, and 2 pairs; 2 rings of 6 and 1 pair; and a ring of 12 and 1 pair, and probably would not have been stable as was the plant discussed above and assigned to *O. elongata*.

Two principles seem to have been important among the evolution of different South American species of this group. In some species extensive genetic changes have taken place without structural modifications of the chromosomal end arrangements. Thus, the strains of *O. peruana*, *O. versicolor*, and *O. scabra* that have been grown in the experimental garden have been chromosomally structurally identical. Other species of series *Renneria* have not deviated far from this chromosomal structural arrangement either, so that a ring of 4 and 5 bivalents was formed both in hybrids between *O. santarii* and *O. versicolor* and also in hybrids between *O. pedunculifolia* and *O. versicolor*.

In many other species structural changes in the form of reciprocal translocations have played a definitive role in the differentiation of species. These translocations have not led to a reduction in fertility because of the regular alternate disjunction of the chromosomes in the rings. As a result, a whole array of chromosomally distinctive lines has arisen from such events. Familiar isolating mechanisms of a geographical, ecological, or physiological nature have in many instances allowed complete speciation following or accompanied by such chromosomal differentiation. In the absence of barriers to hybridization between chromosomally differentiated lines within the group, many such lines have eventually hybridized to produce new complex heterozygous combinations. Indeed, identical combinations have been found, evidently formed more than once at different times in different places. Examples of this are provided by *O. stricta* and *O. picensis*, and these are discussed further under the treatments of the respective species.

As in the chromosomal homozygotes, genetic changes that have occurred in the complex heterozygotes have led eventually to a still further differentiation. The tendency towards the evolution of small-flowered plants in which self-pollination is more and more automatic, regarded in this paper as the ultimate phase in the development of complex heterozygosity, is unmistakable. Despite the extensive suppression of crossing-over in *Oenothera*, the occasional exchange of genes between complexes seems to have had an effect on the course of evolution. An example of this, *O. elongata*, with complexes derived from *O. longituba* and *O. affinis*, has been mentioned. Hybrids between this complex heterozygote and *O. affinis* have shorter capsules than *O. affinis* and this characteristic of *O. longituba* seems to have been introduced by gene exchange in the complex heterozygote. In contrast, *O. picensis* (*Santarius 1549*) is clearly made up of more or less unaltered *O. affinis* and unaltered *O. odorata*. Also, *O. villaricae*, which is known as "*berteriana* Erlangen" in the genetic literature and belongs to series *Clelandia* can be shown to be made up of complexes derived from *O. santarii* and *O. ravenii*.

Among the additional factors of phylogenetic importance among the South American species may be mentioned complex heterozygosity involving more than two species (see species numbers 12, 16c, and 28). A very curious phenomenon involving *O. nana* and *O. punae*, involving a situation in which freely recombined genomes at a single locality seem to be unequally shared by both species, is discussed on p. 611.

An important result of this study is the conclusion that the origin of complex heterozygosity does not depend upon the prior existence of genetically well-differentiated genomes. It can be shown, especially in *O. affinis*, that chromosomally very well-differentiated forms can occur within a single population, be preserved by self-pollination, and eventually give rise to complex heterozygotes which are morphologically essentially identical to the chromosomal homozygotes at that place. (See also Drillisch, 1975: 60–71.) Such complex heterozygotes, since they are from the beginning self-pollinated, may immediately be more or less isolated from other elements of the population and thus in effect give rise to a new and distinctive strain. Thus rings of 14 can arise in a variety of ways in populations of *Oenothera*, either through the hybridization of chromosomally and genetically very well-differentiated strains, or through the gradual accumulation of differences, even within populations.

In contrast to the species of the North American subsect. *Euoenothera*, chromosomal homozygotes are still very well represented among the South American species, even though complex heterozygotes are likewise frequent. These chromosomal homozygotes still have ranges as extensive as those of their complex heterozygous derivatives, and often occur together with them in the same areas (Table 1). The analysis of the South American complex heterozygotes is facilitated by the existence of all of the original participating homozygotes at the present time. The various mechanisms operative in the differentiation of species all can still be observed directly at the present day.

In very actively evolving groups, such as the species of *Oenothera* in South America which are treated in this paper, it is often not possible to delimit sharply defined natural units. Almost all complexes of series *Renneria* and *Allochroa* are interconnected with one another, and they are in a very real sense evolving as an interconnected whole. Connections between species, taken step by step, unify the most distantly related and distictive elements in the group into an intertwined complex of great intricacy but presumably also great evolutionary vigor in responding to the demands of the environment. The two most important elements in the evolution of the group, however, appear to be complex heterozygosity and hybridization. This seems to be particularly true among the South American species of *Oenothera* because of the complete lack of sterility barriers, and because of the chromosomal system which leads easily to the formation of true-breeding hybrids which recombine the characteristics of the parents in various adaptative ways. The frequent instances of sympatric occurrence of the various taxa, with consequent opportunities for hybridization, is documented in Table 1.

In fertile, pair-forming hybrids such as are encountered in many groups of plants, adaptive phenotypes may soon be broken up by recombination and backcrossing, but in stable hybrids, such as self-pollinating complex heterozygotes, it may be preserved. Once a successful complex heterozygote has originated, it may spread in areas beyond those occupied by its homozygous parents, owing to its different adaptive mode, and eventually the parental homozygotes may come to exist only in relatively limited areas, as in the North American subsect. *Euoenothera*.

SYSTEMATIC TREATMENT

Before commencing the formal taxonomic treatment of the South American species of this group, I would like to make a few comments about the descriptions and the way I have employed terminology in them. For the descriptions of individual pubescence types the terms strigillose, villous and glandular-pubescent have been used. All hairs are fundamentally single-celled. "Strigillose" is used to designate short, appressed hairs about 0.1–0.2 mm long; "villous," hairs which stand erect or rise obliquely and are 1–5 mm long; and "glandular-pubescent," hairs 0.1–0.3 mm long which are terminated by a gland. Shorter and appressed

TABLE 1. Sympatric occurrence of taxa of native South American taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.

		peruana	versicolor	lasiocarpa	santarii	longituba	tafien taf	pedunculif	scabra	rubida	tarijensis	recurva	sandiana	nana	mendocinen	odorata	raveni rav	raveni arg	raveni chi	longif gra	longif lon	catharinen	indeco ind	indeco bon	affinis	mollissima	rivadaviae	strict str	strict alt	strict arg	bahia-blan	picens pic	picens cor	picens bon	monteviden	pseudolong	parodi par	parodi str	parodi bra	verrucosa	coquimbens	arequipens	grisea	feathersto	nocturna	magellanic	villaricae	elongata	pseudoelon	cordobensi	siambonens	brevipetal	acuticarpa	tucumanens	punae	lacini pub
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	versicolor			●		●	●	●	●		●	●	●	●											●																							●	●			●			●	
	lasiocarpa		●			●	●	●	●					●											●																														●	
	santarii						●									●									●																					●					●					
	longituba		●	●			●	●	●					●											●																										●		●		●	
	tafien taf		●	●	●	●		●	●					●											●																					●				●	●		●		●	
	pedunculif		●	●		●	●		●					●											●																									●		●	●	●	
	scabra		●	●		●	●	●			●	●	●	●											●																						●	●		●		●		●	
	rubida	●																																						●																
	tarijensis		●						●			●	●	●											●																						●							●	
	recurva		●						●		●		●	●											●																						●							●	
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	raveni rav																				●		●	●	●	●									●		●		●																	
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	affinis		●	●	●	●	●	●	●		●	●			●		●	●		●	●		●	●		●		●		●		●	●		●	●	●		●		●		●			●		●		●	●		●	●	●	
	mollissima																●	●			●		●	●	●									●	●	●	●		●																	
	rivadaviae														●	●																					●								●										
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	picens cor														●			●					●	●	●					●							●									●				●						
	picens bon														●	●		●							●				●	●						●	●																	
	monteviden																●	●			●		●	●	●	●											●		●																	
	pseudolong																				●			●	●	●																													
	parodi par														●		●	●		●	●		●	●	●	●	●			●	●		●	●	●			●	●											●				●		
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	verrucosa	●								●																																														
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CLE	magellanic				●		●								●	●									●		●	●	●		●	●	●															●			●	●					
	villaricae																		●									●	●																	●										
	elongata		●						●		●	●	●	●											●																														
	pseudoelon		●						●				●																																						●				
	cordobensi						●																		●								●				●									●										
	siambonens				●	●	●	●	●																●																					●							●	●		
	brevipetal		●																																														●							
	acuticarpa					●	●	●	●																●																										●			●		
	tucumanens							●																●	●												●														●		●			
	punae		●	●		●	●	●	●		●	●	●	●											●																													
RAI	lacini pub												●																													●		●	●											

villous pubescence is likewise encountered among the South American species of *Oenothera*. All three pubescence types may be present on a single plant.

Description of the form of the vegetative leaves and petals, as well as that of the outline of the buds, capsules, and seeds follows the terminology given by Stearn (1956). Measurements for the buds are given for those just about to open. The length is given exclusive of the floral tube. Measurements of the sepals are given at the same stage. Length of the ovary is given at the stage when the flowers have just opened.

The asterisks on the chromosomal configurations mentioned at the end of the description correspond with those given in the lists of plants cultivated in the experimental garden at Düsseldorf.

The geographical distributions are in general given in broad terms, since many of the ranges, especially those involving the species occurring in the high mountains, are insufficiently known. Further sampling will be necessary before they can be specified more precisely.

Finally, it is important to add a word about the duration of the plants. Often in the literature and on the labels of specimens, plants of this group are said to be "perennial." In most instances I have not been certain how to treat these observations, since in our experience all species appear to be either biennial (especially the rosette-forming ones) or annual. Probable exceptions, and species that may truly be perennial, are *O. nana* and *O. punae.* I have not been able in any case to find on a herbarium specimen any plant parts indicating that the individuals had flowered more than once, or structures such as overwintering buds which might have indicated a true perennial habit. Structures which might have seemed to have been formed during an earlier flowering cycle could in all cases be attributed to the activities of sheep or other grazing animals. There seems to be no indication that any of these plants are generally perennial, although when they are cropped off by an animal or cut back in a stage of active growth, new shoots will often form freely from the base and a second flowering will take place within the same season. In Düsseldorf we often employed this device in order to synchronize the blooming of two different species which might not otherwise have flowered at the same time.

OENOTHERA sect. *OENOTHERA*

Three subsections are represented in South America, and may be separated by the following key:

1. Seeds prismatic; infrequent naturalized plants .... C. Subsect. *Euoenothera* (p. 615)
1'. Seeds not prismatic; mostly native.
    2. Buds nodding or floral tubes of the oldest buds curved upward .... B. Subsect. *Raimannia* (p. 612)
    2'. Buds erect, the floral tubes not curved upward .... A. Subsect. *Munzia* (p. 443)

A. Subsection MUNZIA

Oenothera sect. **Oenothera** subsect. **Munzia** Dietrich, subsect. nov.

Plantae annuae vel biennes, erectae vel prostratae, rosulares vel erosulares; gemmae non nutantes, tubus floralis non sursum curvatus. Habitat in America Meridionalis.

Annual or biennial plants, erect or prostrate, forming a rosette or growing directly from seed without one, or remaining permanently and flowering as a rosette. Plants unbranched or with a branched main stem and decumbent, arching, or straight side branches arising from the rosette, a few cm to 2 m tall. Rosette 5 cm (*O. nana*) to 70 cm (*O. longituba*) in diameter. Main stem 0.3–2 cm thick. Plants (1) very densely to sparsely strigillose and thickly to sparsely appressed to erect long-villous; (2) very densely to sparsely strigillose, densely to sparsely long-villous, and very sparsely to sparsely glandular-pubescent; (3) very densely to very sparsely appressed or erect long-villous, densely to very sparsely glandular-pubescent; or (4) densely short-villous and glandular-pubescent. Rosette leaves linear, elliptic, or oblanceolate, long or short acute, gradually narrowed to the petiole or sessile, attenuate to acute at the base, 2.5–35 cm long, 0.2–6 cm wide; cauline leaves linear, elliptic, lanceolate, or oblanceolate, acute, sessile, acute to truncate at the base, or distinctly short-petiolate and narrowly cuneate at the base, 2.5–25 cm long, 0.1–4 cm wide; bracts linear, elliptic or lanceolate to ovate, acute to almost obtuse, sessile and acute to subcordate at the base or distinctly short-petiolate and attenuate at the base, 1–12 cm long, 0.1–3 cm wide, longer or shorter than the capsule they subtend or ± the same length; leaves regularly or irregularly to sparsely toothed, the teeth obtuse or acute, plane or undulate, the surface sometimes flecked wih black (*O. nana*). Inflorescence simple or branched, dense or rather sparse. Floral tube 0.5–12 cm long, sometimes flecked with red or reddish brown. Buds oblong, elliptic to rotund or lanceolate to ovate in outline, 0.4–3.5 cm long, 0.15–1 cm thick, often red striped at the junction of the sepals or also along the midribs of the sepals. Sepals green or yellow to greenish yellow, often flushed with red, sometimes flecked with dark red or reddish brown; sepal teeth 1–4 mm long, erect or divergent. Petals broadly elliptic or obovate to broadly obovate, rotund or retuse, 0.5–4.5 cm long, yellow to straw colored, sometimes flushed with red near the base and along the nerves, or completely red. Anthers 0.2–1.5 cm long, yellow, sometimes reddish. Filaments 0.2–2.5 cm long, yellow, sometimes reddish. Style 1–14 cm long, surrounded by the anthers in bud or exceeding them in length. Stigma lobes 4, 1–10 mm long. Ovary 0.8–1.5 cm long, cylindrical. Capsule ovate or oblong in outline, narrowed toward the apex, occasionally swollen below the apex (*O. affinis*), fused with the subtending bract at the base or free, occasionally clearly stalked (*O. verrucosa*), erect and appressed to the stem or spreading sharply or even at a right angle to it, 1–6 cm long, 2–10 mm thick; valves of the capsule separating from the placenta when ripe, spreading or curving inward or outward. Seeds 0.8–2 mm long, 0.5–1 mm thick, ± bluntly angled or elliptic to rotund in outline, light brown to dark brown or black, sometimes dark flecked. Self-compatible and outcrossed or self-pollinated. Chromosomally homozygous or permanently heterozygous and isogamous or semiheterogamous. Gametic chromosome number, $n = 7$ (7 bivalents, ring of 14, or intermediate configurations at meiotic metaphase I).

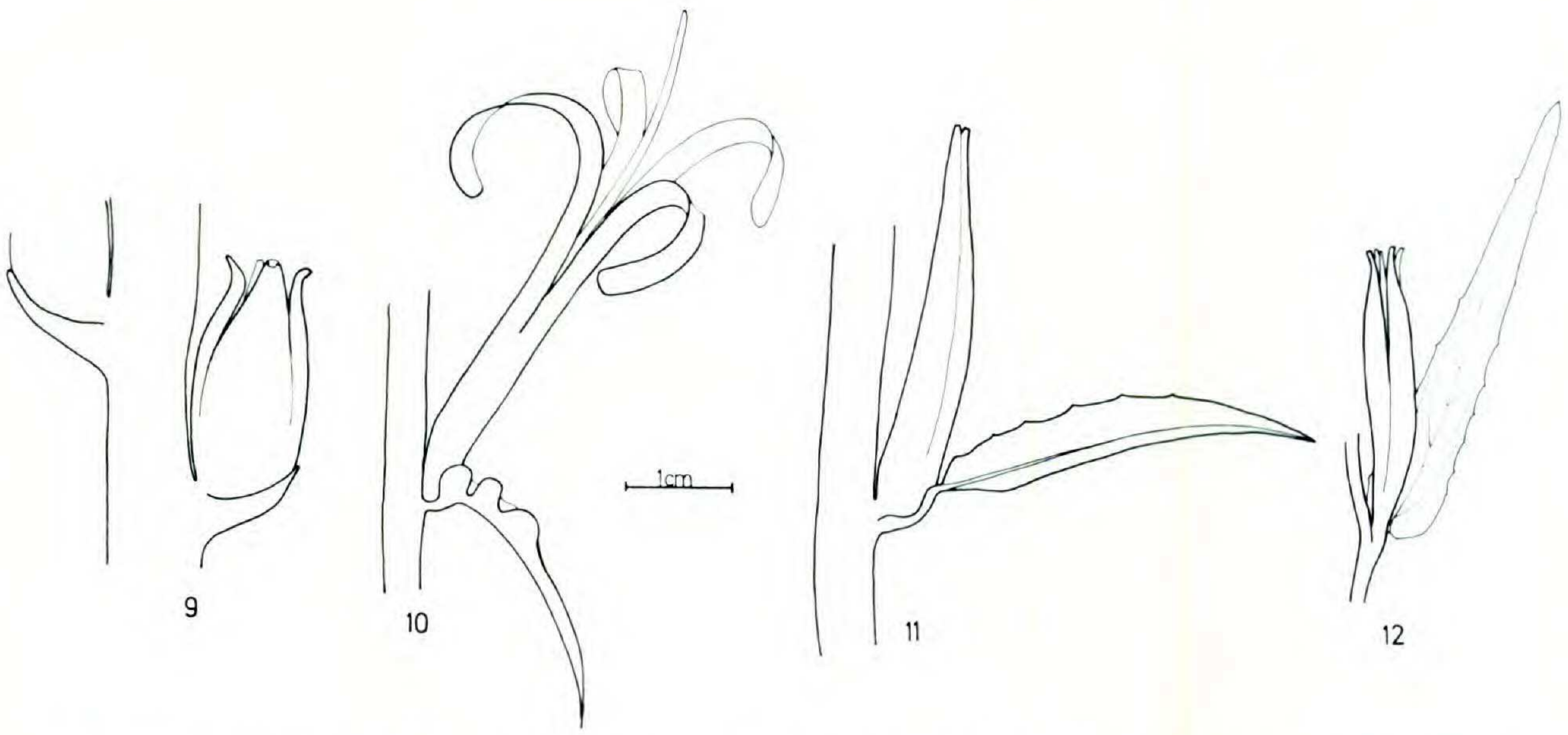
Type species: *Oenothera odorata* Jacq.

Distribution (Fig. 7): All species occur in more or less open plant communities from sea level to almost 5,000 m elevation in the Andes (*O. nana*). Among the sorts of places they grow are seacoasts, dunes and other sandy places, gravelly fields, dry watercourses; fields, meadows, and pastures; open shrublands and woods; grassy and shrub-steppes, Andean puna; banks of streams; edges of roads and disturbed places. The subsections occur nearly throughout the southern half of South America, and northward along the Andes to Colombia; some of its species are widely cultivated and naturalized on other continents.

This subsection is dedicated to P. A. Munz (1892–1974), lifelong student of Onagraceae.

Key to the Series of Subsect. *Munzia*

1. Capsule urn-shaped (Fig. 9), gradually narrowed toward the tip, erect or standing out at a right angle from the stem, 4–9 mm thick at the base and with the subtending



FIGURES 9–12. Capsules representative of the series of *Oenothera* subsect. *Munzia*.—9. *O. scabra* subsp. *scabra* (*Renneria*).—10. *O. rivadaviae* (*Allochroa*).—11. *O. acuticarpa* (*Clelandia*).—12. *O. verrucosa* (*Allochroa*).

leaf distinctly fused to it; valves of the capsule spreading after seeds are shed .... Series *Renneria* (p. 450)

1′. Capsule ± cylindrical (Figs. 10–12), at most tapering toward the apex, erect or standing out from the stem, 1.5–4 mm thick, usually not or slightly fused with the subtending bract; valves of the capsule spreading or curved inward or outward after seeds are shed.
  2. Capsule cylindrical (Fig. 10), rarely enlarged in the upper third or somewhat petiolate, not fused with the subtending bract .... Series *Allochroa* (p. 489)
  2′. Capsule generally gradually narrower upward from a broad base (Fig. 11), evidently fused with the subtending bract for a short distance .. Series *Clelandia* (p. 585)

KEY TO THE SPECIES OF *Oenothera* SECT. *Oenothera* IN SOUTH AMERICA

1. Seeds prismatic Subsect. (*Euoenothera*).
  2. Floral tube 2–5 cm long.
    3. Petals 3.5–5 cm long .... 48. *O. erythrosepala*
    3′. Petals 1–2.5 cm long .... *O. biennis* (p. 618)
  2′. Floral tube 1–1.8 cm long .... 49. *O. villosa* subsp. *strigosa*
1′. Seeds not prismatic.
  4. Buds nodding or the floral tube of the oldest buds curved upward Subsect. (*Raimannia*).
    5. Petals 0.5–1.5 cm long.
      6. Sepals often flecked with red; apices of the sepals 0.5–1 mm long .... 46a. *O. laciniata* subsp. *pubescens*
      6′. Sepals never flecked; apices of the sepals 1–2 mm long .... 46b. *O. laciniata* subsp. *laciniata*
    5′. Petals 2.5–5 cm long .... 47. *O. drummondii*
  4′. Buds not nodding; floral tubes not curved upward Subsect. (*Munzia*).
    7. High mountain plants of very condensed habit, either flowering in the rosette or forming short, prostrate side branches; capsules 1–2 cm long.
      8. Plants forming a rosette only, rarely with short side branches; capsules standing out at right angles from the stem .... 13. *O. nana*
      8′. Plants with prostrate side branches 5–20 cm long; capsule ± appressed to the stem .... 45. *O. punae*
    7′. Plants neither rosette-forming nor prostrate, or taller than 15 cm, erect or prostrate, but if prostrate, then the capsules more than 2 cm long.

9. Capsule urn-shaped, gradually narrowed toward the tip, erect, 4–9 mm thick at the base and with the subtending leaf fused to it; valves of the capsule spreading after seeds are shed; exclusively mountain plants (series *Renneria* in large part).

10. Floral tube 6–10 cm long; flowers exceeding the apex of the stem in length.

11. Plants forming a rosette, with a crowded inflorescence; pubescence strigillose and erect villous; petals 2.5–4.5 cm long .... 5. *O. longituba*

11′. Plants not forming a rosette, with a more slender and lax inflorescence; pubescence strigillose and appressed villous; petals 2–3 cm long .... 11. *O. recurva*

10′. Floral tube 1.2–5.5 cm long; flowers mostly not exceeding the apex of the stem in length.

12. Floral tube 2.5–5.5 cm long.

13. Plants with appressed and erect pubescence, sometimes also glandular-pubescent.

14. Buds narrowly lanceolate to oblong in outline; petals 2–3.5 cm long; seeds mostly flecked with dark spots, 0.8–1.3 mm long; plants glandular pubescent at times .... 8. *O. scabra*

14′. Buds lanceolate in outline; petals 1.5–2.5 cm long; seeds almost always immaculate; plants never glandular pubescent .... 12. *O. sandiana*

13′. Pubescence all appressed.

15. Upper bracts with red margins; petals often reddish near the base and along the veins; seeds dark brown to almost black, 1.3–1.5 mm long .... 10. *O. tarijensis*

15′. Bracts without red margins; petals entirely yellow; seeds light brown to dark brown, flecked with reddish brown, 0.8–1.2 mm long.

16. Leaves regularly and acutely serrate; bracts evidently petiolate; seeds 0.8–1 mm long .... 7. *O. pedunculifolia*

16′. Leaves irregularly and bluntly serrate; bracts sessile; seeds 1–1.2 mm long .... 6. *O. tafiensis*

12′. Floral tube 1.2–2.5 cm long.

17. Plants with both appressed and erect pubescence.

18. Plants 1–3.5 dm tall; floral tube 1.5–2 cm long; petals 1.5–2 cm long, reddish at the base and along the veins ... 3. *O. lasiocarpa*

18′. Plants 5–12 dm tall; floral tube 2–2.5 cm long; petals 2–3 cm long, entirely yellow .... 4. *O. santarii*

17′. Plants with appressed pubescence only.

19. Bracts reddish along the margins; petals red or with a red spot at the base and reddish along the veins .... 2. *O. versicolor*

19′. Bracts not reddish; petals entirely yellow.

20. Plants forming a rosette; petals 1.5–2.5 cm long; capsule 6–9 mm thick .... 1. *O. peruana*

20′. Plants not forming a rosette; petals 0.8–1.2 cm long; capsule 4–5 mm thick .... 9. *O. rubida*

9′. Capsule ± cylindrical, at most tapering toward the apex, erect or standing out from the stem, 1.5–4 mm thick, rarely somewhat thicker, usually only indistinctly fused with the subtending leaf if at all; valves of the capsule spreading or curved inwardly or outwardly when ripe after seeds are shed.

21. Floral tube 7–11(–13) cm long.

22. Plants forming a rosette; pubescence thick and shaggy; bracts shorter than the capsule they subtend .... 17. *O. longiflora*

22′. Plants not forming a rosette; pubescence soft; bracts longer than the capsule they subtend.

23. Bracts cultrate to narrowly lanceolate; capsule 2.5–4 cm long, 3–4 mm thick, somewhat enlarged in the upper third; seeds 1.5–2 mm long .... 20. *O. affinis*

23′. Bracts lanceolate to narrowly ovate; capsule 2–3 cm long, 4–5 mm thick, not enlarged above; seeds 1.1–1.5 mm long .... 38. *O. elongata*

21′. Floral tube at most 6.5 cm long.

24. Capsule narrowed at the base and at the apex, apparently stipitate; valves of the capsule spreading when seeds are shed; annual plants, mostly less than 3 dm tall.

25. Plants mostly unbranched; leaves remotely and bluntly serrate; floral tube 0.6–1.1 cm long; seeds 1.5–1.7 mm long, dark brown to almost black .... 29. *O. verrucosa*

25′. Plants branched; leaves sinuate-toothed; floral tube 1–3 cm long; seeds 1–1.3 mm long, brown .... 31. *O. arequipensis*

24′. Capsule not narrowed at the base; valves curving when seeds are shed.

26. Leaves with long, narrow teeth, these often secondarily toothed, or leaves remotely and bluntly serrate; valves of the capsule curving inward when seeds are shed; seeds narrowly elliptic in outline, 1.2–1.6 mm long, 0.4–0.5 mm thick .... 30. *O. coquimbensis*

26′. Leaves without long, narrow teeth; valves of the capsule curving outward or spreading when seeds are shed; seeds elliptic to broadly elliptic in outline.

27. Plants with exclusively appressed pubescence.

28. Petals 2.5–4.5 cm long .... 33. *O. featherstonei*

28′. Petals less than 2.5 cm long.

29. Bracts linear .... 14. *O. mendocinensis*

29′. Bracts not linear.

30. Capsule 3–4.5 cm long, 3–4 mm thick .... 24. *O. bahia-blancae*

30′. Capsule less than 3 cm long, 2–3.5 mm thick.

31. Capsule shorter than the subtending bract .... 28b. *O. parodiana* subsp. *strigulosa*

31′. Capsule longer than the subtending bract.

32. Bracts lanceolate to ovate, truncate to subcordate at the base; leaves with blunt teeth; seeds elliptic in outline, 1.3–1.5 mm long, 0.5–0.7 mm thick .... 32. *O. grisea*

32′. Bracts narrowly elliptic to lanceolate, attenuate at the base; leaves mostly sinuate-toothed; seeds broadly elliptic in outline, 1.3–1.8 mm long, 0.8–0.9 mm thick .... 34. *O. nocturna*

27′. Plants with some erect pubescence.

33. Bracts linear .... 14. *O. mendocinensis*

33′. Bracts not linear.

34. Petals 2.5–5 cm long.

35. Bracts narrowly oblong to lanceolate, rounded at the base; plants not forming a rosette .... 18. *O. catharinensis*

35′. Bracts lanceolate to narrowly ovate, truncate to subcordate at the base; plants forming a rosette.

36. Bracts longer than the capsule they subtend .... 15. *O. odorata*

36′. Bracts shorter than the capsule they subtend, or at most subequal to it.

37. Bracts usually only half as long as the capsule they subtend, or even shorter; floral tube (3–)3.5–5.5 cm long; capsule 2.5–3.5 cm long; seeds 1.3–1.5 mm long .... 16a. *O. ravenii* subsp. *ravenii*

37′. Bracts more than half as long as the capsule they subtend; floral tube 2.5–3.5 cm long; capsule 3.5–5 cm long; seeds 1.5–1.8 mm long .... 23b. *O. stricta* subsp. *altissima*

34′. Petals at most 2.5 cm long.

38. Capsule 1–1.5 cm long .... 42. *O. brevipetala*

38′. Capsule longer.

39. Capsule 1.5–2.5 mm thick.

40. Plants exclusively short-villous and glandular-pubescent, appearing glabrous when viewed without a lens .... 19b. *O. indecora* subsp. *bonariensis*

40′. Plants with erect, long villous pubescence in part.

41. Capsule 3.5–6 cm long .... 22. *O. rivadaviae*

41′. Capsule at most 3 cm long.

42. Bracts only half as long as the capsule they subtend or shorter, truncate to subcordate at the base .... 28a. *O. parodiana* subsp. *parodiana*

42′. Bracts subequal to or longer than the capsule they subtend.

43. Plants strigulose, villous, and glandular-pubescent; bracts evidently longer than the capsule they subtend .... 44. *O. tucumanensis*

43′. Plants only villous and glandular-pubescent; bracts subequal to or shorter than the capsule they subtend.

44. Plants forming a rosette, ± villous; sepals often flecked with dark red; capsule 1.5–2 mm thick; seeds 1–1.3 mm long .... 19a. *O. indecora* subsp. *indecora*

44′. Plants not forming a rosette, densely villous; sepals not flecked with red; capsule 2–2.5 mm thick; seeds 1.5–1.6 mm long .... 26. *O. montevidensis*

39′. Capsule 3–4 mm thick.

45. Bracts longer than the capsule they subtend.

46. Plants only villous and glandular-pubescent; capsule standing out obliquely from the stem.

47. Plants very densely long-villous.

48. Bracts rounded to truncate at the base, those towards the tip of the stem erect and somewhat imbricate .... 21. *O. mollissima*

48′. Bracts truncate to subcordate at the base, spreading .... 25. *O. picensis*

47′. Plants not very densely long-villous .... 25. *O. picensis*

46′. Plants strigillose and villous; in part also glandular-pubescent; capsule ± erect.

49. Plants densely long-villous; petals 0.8–1.3 cm long .... 39. *O. pseudoelongata*

49′. Plants with various pubescence; petals at least 1.5 cm long.

50. Plants forming a rosette; floral

tube 1.3–2.5(–3) cm long; seeds immaculate.

51. Bracts evidently longer than the capsule they subtend, without red margins; capsule 2.5–4 cm long; seeds 1.4–2 mm long ...... 35. *O. magellanica*

51′. Bracts slightly longer than to shorter than the capsule they subtend, with red margins; capsule 2–3 cm long; seeds 1.1–1.5 mm long ... 36. *O. villaricae*

50′. Plants not forming a rosette; floral tube 3–6 mm long; seeds flecked with reddish brown.

52. Bracts only a little longer than the capsule they subtend or shorter, mostly with red margins ...... 41. *O. siambonensis*

52′. Bracts evidently longer than the capsule they subtend, without red margins ...... 43. *O. acuticarpa*

45′. Bracts subequal to or shorter than the capsule they subtend.

53. Capsule suberect.

54. Plants forming a rosette; seeds immaculate.

55. Floral tube 2–3 cm long ...... 36. *O. villaricae*

55′. Floral tube 4–4.5 cm long ...... 37. *O. hechtii*

54′. Plants not forming a rosette; seeds flecked with reddish brown.

56. Floral tube 1.5–2.5 cm long; capsules with the 4 valves evidently free and crenate at the apex ...... 40. *O. cordobensis*

56′. Floral tube 3–5.5 cm long; capsule without evidently free valves ...... 41. *O. siambonensis*

53′. Capsule standing out from the stem.

57. Petals at most 1.5 cm long.

58. Plants not forming a rosette; floral tube 3–4.5 cm long ...... 25b. *O. picensis* subsp. *cordobensis*

58′. Plants forming a rosette; floral tube at most 3 cm long.

59. Capsule 3–4.5 cm long ...... 24. *O. bahia-blancae*

59′. Capsule 2.5–3 cm long.

60. Floral tube 1.8–3 cm long; buds 10–17 mm long; petals 1.2–2 cm long ...... 16b. *O. ravenii* subsp. *argentinae*

60′. Floral tube 1–2 cm long; buds 5–8 mm long; petals 0.7–1.2 cm long ...... 28a. *O. parodiana* subsp. *parodiana*

57′. Petals more than 1.5 cm long.

61. Floral tube more than 4 cm long.

62. Floral tube usually more than 4.5 (–6.5) cm long; buds narrowly oblong to oblong in outline .. 27. *O. pseudolongiflora*

62′. Floral tube at most 4.5 cm long; buds lanceolate in outline.

63. Upper bracts with arched incurved apices; plants with long, bristly hairs, especially below .... 28c. *O. parodiana* subsp. *brasiliensis*

63′. Upper bracts plane; plants strigillose, especially below, never with long, bristly hairs .... 23a. *O. stricta* subsp. *stricta*

61′. Floral tube less than 4 cm long.

64. Bracts at most half the length of the capsule they subtend .... 16. *O. ravenii*

64′. Bracts more than half the length of the capsule they subtend.

65. Upper bracts erect .... 23c. *O. stricta* subsp. *argentinae*

65′. Upper bracts spreading.

66. Rosette leaves 0.8–1.3 cm wide; cauline leaves 0.6–1 cm wide; bracts 0.7–1.2 cm wide; seeds 1.5–1.8 mm long .... 23a. *O. stricta* subsp. *stricta*

66′. Rosette leaves 1.2–3 cm wide; cauline leaves 1–2.5 cm wide; bracts 1.2–2 cm wide; seeds 1.2–1.5 mm long .... 28c. *O. parodiana* subsp. *brasiliensis*

Series I. RENNERIA

Oenothera sect. **Oenothera** subsect. **Munzia** series **Renneria** (Fischer) Dietrich, stat. nov. Based on *Oenothera* subgen. *Renneria* Fischer, Feddes Repert. Spec. Nov. Regni Veg. 64: 233. 1962

Onagra sensu Krause, Repert. Spec. Nov. Regni Veg. 1: 167. 1905.

Oenothera § *Euoenothera* sensu Munz & Johnston, Contr. Gray Herb. 75: 17. 1925, pro parte.

Oenothera subgen. *Euoenothera* sensu Munz, Physis 11: 280. 1933; Revista Univ. (Santiago) 22: 262. 1937, pro parte; sensu Hagen, Indiana Univ. Publ. Sci. Ser. 16: 306. 1950, pro parte.

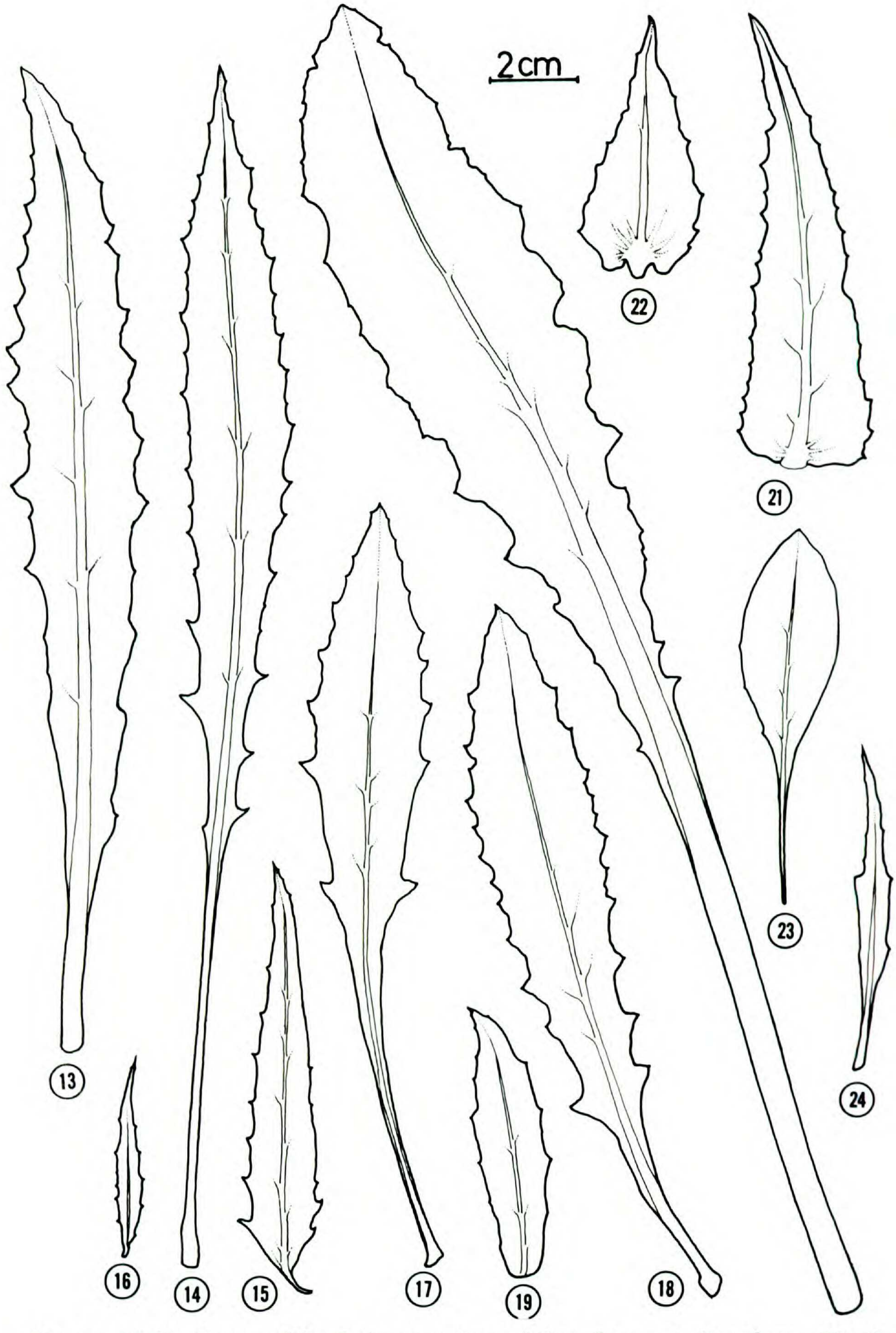
Oenothera subgen. *Raimannia* Munz, Physis 11: 279. 1933, pro parte; Amer. J. Bot. 22: 645. 1935, pro parte.

Erect annual or biennial, possibly sometimes perennial, herbs, forming a rosette or elongating soon after germination, sometimes flowering in the rosette, simple or with a ± branched main stem and arcuate to oblique side branches arising from the rosette; plants less than 1 dm to 15 dm tall. Plants very densely to sparsely strigillose, often also appressed or erect long-villous, rarely glandular-pubescent. Rosette leaves linear to lanceolate, acute, narrowed gradually or ± abruptly to the petiole, rarely sessile, 2.5–35 cm long, 0.3–6 cm wide; cauline leaves linear, elliptic or lanceolate, acute, sessile and acute to truncate at the base, or narrowly cuneate at the base and with a long or short petiole, 3–20 cm long, 0.3–3 cm wide; bracts linear, elliptic or lanceolate, acute, sessile and acute to subcordate at the base or attenuate at the base and with a long or short petiole, 3–12 cm long, 0.3–2.5 cm wide, longer than the capsules they subtend; leaves ± regularly or irregularly serrate, plane or undulate at the margins, sometimes (in *O. nana*) flecked with black. Inflorescence simple or branched, mostly crowded; flowers mostly obliquely erect, (1–)2–6 opening toward the apex each day. Floral tube 0.5–10 cm long, usually curved. Buds oblong to narrowly ovate in outline, 0.4–3.5 cm long, 3–8 mm thick, often with red stripes at the junction of the sepals with the floral tube, and sometimes also along the midveins. Sepals green, yellowish, or yellowish green, often flushed with red; apices of the sepals 1–4 mm long, erect or divergent. Petals very broadly obovate, rounded or retuse, 0.5–4 cm long, yellow or bright yellow, sometimes flushed with red along the veins and at the base, or completely red. Ovary 0.8–1 cm long. Capsule oblong or lanceolate to ovate in outline, 1–3 cm long, 3–10 mm thick, erect and ± appressed to the stem, or (in *O. nana*) standing out at right angles from the prostrate stems, evidently fused with the bracts; valves spreading apart in dehiscence or slightly incurved at the apex only. Seeds ± obtusely angular, rounded and elliptic in outline, 0.8–1.7 mm long, 0.5–1 mm thick, light brown to dark brown or black, sometimes with darker flecks. Self-compatible; outcrossing or self-pollinating chromosomal homozygotes or self-pollinating complex heterozygotes. Gametic chromosome number, $n = 7$ (bivalents, ring of 14, or intermediate configurations at meiotic metaphase I).

Lectotype species: *Oenothera versicolor* Lehm: = *O. campylocalyx* Koch & Bouché.

Distribution (Fig. 7): All species of this subsection are exclusively mountain plants and occur at elevations from 1,500 to 5,000 m, rarely lower. They occur at these elevations in the Cordillera Occidental and Cordillera Oriental of Peru from the province of Lambeyeque southward a short distance over the Chilean border. In the Bolivian and Argentine Andes, the group ranges along the eastern flanks southward to Mendoza. Disjunct stations occur in the Sierra of Córdoba and in the Andes of Ecuador near Quito, the latter probably resulting from the naturalization of cultivated plants.

The characteristic aspect of the plants of this section results from their thick stems, sometimes up to 2 cm in diameter, crowded inflorescences, and obliquely ascending flowers with somewhat curved floral tubes. Most diagnostic, however, are the erect, urn-shaped or broadly cylindrical capsules (Fig. 9). The



FIGURES 13–24. Leaves of South American taxa of *Oenothera* sect. *Oenothera*.—13. Rosette leaf of *O. peruana* (Peru, Arequipa, *Santarius 2090*).—14–16. Rosette leaf, cauline leaf, and bract of *O. versicolor* (Bolivia, Cochabamba, *Diers in 1959*).—17–19. Rosette leaf, cauline leaf, and bract of *O. tafiensis* subsp. *tafiensis* (Argentina, Tucumán, *Santarius 1733*).—

three first species are annual, although potentially overwintering as a rosette and therefore biennial, whereas *O. santarii* and *O. longituba* are obligate biennials in nature, although flowering the first year in cultivation. These five species have somewhat angular seeds which are dark brown or black.

Oenothera scabra forms only a few leaves near the base on germination, and then grows into a branching plant without forming a rosette. Its seeds are rounded in outline, smaller than those of the first-listed and presumably more generalized species of the series, light brown, and flecked. *Oenothera tafiensis* and *O. pedunculifolia* can be considered intermediate between *O. scabra* and the remaining species; thus *O. tafiensis* subsp. *tafiensis* resembles *O. peruana* in habit, but has small flecked seeds. In *O. tafiensis* subsp. *parviflora* and *O. pedunculifolia*, both also with flecked seeds, the plants bolt from a rosette of limited size and resemble *O. scabra* in habit.

1. **Oenothera peruana** Dietrich, sp. nov.—Figs. 13, 102, 168.

Herba annua vel biennis, erecta, rosulata, 5–10 dm alta, simplex vel caulis principalis ramosus et ramis oblique e rosula ascendentibus. Herba tota dense strigulosa, circum inflorescentiam pilis longis adpressis praedita. Folia rosulae angustissime elliptica vel anguste oblanceolata, acuta, lamina in petiolum brevem gradatim decrescens, 15–20 cm longa, 2–5 cm lata; folia caulina linearia vel cultrata ad anguste lanceolata, acuta, basi acuta, 6–20 cm longa, 1–3 cm lata, breviter petiolata; bractea linearia vel anguste obovata, acuta, basi truncata, sessilia, 3–6 cm longa, 0.8–2 cm lata; folia omnia irregulariter ± serrata. Inflorescentia simplex. Tubus floralis 1.2–2 cm longus. Gemmae ambito lanceolatae, 1.5–2.5 cm longae, 5–7 mm crassae, griseovirides vel flavovirides; apices sepalorum ca. 2 mm longi, erecti. Petala latissime obovata, floride lutea, post anthesem decolorata, 1.5–2.5 cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato. Ovarium 7–10 mm longum. Capsula 2–3 cm longa, 6–9 mm crassa, maturitate brunnea. Semina obtuse angulata, 1.2–1.7 mm longa, 1–1.2 mm crassa, nigra. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice admodem homozygotica.

Erect annual or biennial herb, forming a rosette, 5–10 dm tall. Main stem simple or somewhat branched, with side branches arising obliquely from the rosette. Entire plant densely strigillose, in the region of the inflorescence also with appressed long-villous pubescence. Rosette leaves very narrowly elliptic to narrowly oblanceolate, acute, gradually narrowed to the petiole, 15–20 cm long, 2–5 cm wide; cauline leaves linear or cultrate to narrowly lanceolate, acute, acute at the base, 6–20 cm long, 1–3 cm wide, with a short petiole; bracts linear to narrowly obovate, acute, truncate at the base, sessile, 3–6 cm long, 0.8–2 cm wide; all leaves irregularly and ± prominently serrate, plane or undulate at the margins. Inflorescence unbranched. Floral tube 1.2–2 cm long. Buds lanceolate in outline, 1.5–2.5 cm long, 5–7 mm thick, gray green or yellowish green; apices of sepals erect, ca. 2 mm long. Petals very broadly obovate, bright yellow, fading after anthesis, 1.5–2.5 cm long. Anthers 6–9 mm long. Filaments 8–11 mm long. Style long, the style held above the anthers at anthesis, 2–4.5 cm long. Stigma lobes 4–7 mm long. Ovary 7–10 mm long. Capsule 2–3 cm long,

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20–22. Rosette leaf, cauline leaf, and bract of *O. santarii* (Argentina, Mendoza, *Santarius 1430*).—23. Rosette leaf of *O. tafiensis* subsp. *parviflora* (Argentina, Tucumán, *Göpel in 1961*).—24. Rosette leaf of *O. nana* (Peru, Puno, *Santarius 2045*).

6–9 mm thick, dark brown to very dark brown when ripe. Seeds 1.2–1.7 mm long, 1–1.2 mm thick, obtusely angular, black. Self-compatible but outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 8 and 3 bivalents **, ring of 12 and 1 bivalent ***, or ring of 14**** at meiotic metaphase I). Flowering time: December–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 25 July 1972. Source: Peru, Dep. Arequipa, moist slope and edge of an irrigation ditch 19 km behind Arequipa at road to Chihuata/Puno, 2,700 m, 13 Apr. 1968, *K. A. Santarius 2090* (MO-2155406, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 225): Very local in the Andes of south Peru and north Chile, 2,500–3,300 m elevation.

Specimens examined from cultivated plants:

PERU. AREQUIPA: Ca. 19 km behind Arequipa at the road to Chihuata/Puno, 2,700 m, *Santarius 2075*, *2088****, *2090**, *2091**, *2096****, *2098**, *2102**, *2103**, *2104****, *2106**, *2107**, **, *2108***** (DUSS, *2098* also CTES, *2075*, *2088*, *2090*, *2096*, *2098*, *2106*, *2108* also MO; *2090*, *2098*, *2106* also M).

Additional specimens examined:

PERU. APURIMAC: Abancay, 3,100 m, *Iltis & Ugent 695* (UC). AREQUIPA: Chihuata, 20 km E of Arequipa, *Munz 15539* (POM). Pichu-Pichu, 3,300 m, *Sandemann 3778* (K). Cailloma, 3,180 m, *Lopez 284* (RSA).

CHILE. TARAPACÁ: Mamiña, *Pfister 9451* (CONC).

In contrast to all of the following species, *O. peruana* has clearly angled seeds. On the basis of this characteristic, it seems to stand closest to the common origin of the South American species of sect. *Oenothera* with the North American ones that have been called subgen. *Euoenothera*.

It is possible that complex heterozygotes arise from time to time in the zone of overlap between *O. peruana* and *O. versicolor*, since some plants with a ring of 14 (*Santarius 2108*) are intermediate between these species. These plants are morphologically indistinguishable from *O. peruana*, and are not taken as representing an independent species. Plants with smaller rings of chromosomes are regarded as hybrids between chromosomally structurally differentiated individuals of *O. peruana*.

2. **Oenothera versicolor** Lehm., Ind. Sem. Hort. Bot. Hamb. 7. Dec. 1855; Linnaea 28: 359. 1856.—FIGS. 14–16, 103–104, 169.

O. campylocalyx Koch & Bouché, Ind. Sem. Hort. Berol. App. 17. 1856. LECTOTYPE: Cultivated in Berlin Botanical Garden, 1832, ex herb. Kunth, source unknown (B, destroyed; POM, fragments and photographs).

O. coccinea Britton, Bull. Torrey Bot. Club 17: 213. 1890. LECTOTYPE: Bolivia, Dep. Potosí, Ingenio del Oro, 3,280 m, Mar. 1886, *H. H. Rusby 1815* (NY); Munz & Johnston, Contr. Gray Herb. 75: 22. 1925.

Onagra fusca Krause, Repert. Spec. Nov. Regni Veg. 1: 167. 1905. TYPE: Peru, Dep. Ancash, near Pampa Romas, between Samanco and Caraz, among herbs, especially grasses and shrubs, 3,200–3,500 m, *A. Weberbauer 3211* (B, destroyed in World War II, POM, photograph).

Oenothera campylocalyx sensu Macbride, Field Mus. Nat. Hist., Bot. Ser., 13(4): 535. 1941, pro parte.

O. rubida sensu Macbride, Field Mus. Nat. Hist., Bot. Ser., 13(4): 540. 1941, pro parte.

O. kopenhagensis Latzel, Biol. Zentralbl. 86. 409. 1967. Invalid name. = *Oenothera versicolor* Lehm.

O. campylocalyx sensu Munz, Opera Bot., Ser. B, 3: 39. 1974, pro parte.

Erect annual or biennial herb, forming a rosette, 5–8 dm tall. Plants unbranched or with a scarcely branched main stem and with arcuate-ascending side branches from the rosette. Lower portion of plants sparsely strigillose, becoming densely so in the region of the inflorescence, where also with an admixture of appressed and erect long-villous pubescence. Rosette leaves narrowly lanceolate, acute, gradually narrowed to the petiole, 20–25 cm long, 1.5–3.5 cm wide; cauline leaves very narrowly elliptic to narrowly lanceolate, acute, narrowly cuneate at the base, 8–12 cm long, 0.6–2 cm wide, sessile or with a short petiole; bracts linear to very narrowly elliptic or narrowly lanceolate, acute, acute to truncate at the base, 5–10 cm long, 0.5–2 cm wide; leaves plane or undulate at the margins, ± regularly serrate with acute or rounded teeth, the margins reddish, especially in the bracts of the young buds. Inflorescence mostly unbranched. Floral tube 1.2–2.5 cm long. Buds lanceolate in outline, 1.5–2 cm long, 5–7 mm thick when mature, reddish at the junction of the sepals with the floral tube; apices of the sepals erect or divergent, 2–3 mm long. Petals very broadly obovate, rounded or retuse, 1.2–2 cm long, yellow, red near the base and along the veins or entirely red. Anthers 5–8 mm long. Filaments 6–10 mm long. Style mostly short, the anthers shedding pollen directly on the stigma at anthesis, but sometimes longer, the stigma elevated above the anthers, 2–3.5 cm long. Stigma lobes 2.5–4.5 mm long. Ovary 8–10 mm long. Capsule 1.5–3 cm long, 5–9 mm thick, glabrescent, dark brown to very dark brown when ripe. Seeds 1–1.3 mm long, 0.6–0.7 mm thick, ± obscurely angled, dark brown to black. Self-compatible; self-pollinating or outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: Ecuador and Peru, December–June; Bolivia, October–May; Argentina, October–April.

Type: not seen. The original description clearly indicates the species described here.

Distribution (Fig. 226): Andes of Peru, Bolivia, and Argentina from the department of Ancash in Peru through Bolivia to the province of La Rioja in Argentina, 2,000–4,500 m elevation. The occurrence in Ecuador (Pinchincha Prov.) might represent the establishment of adventive plants.

Specimens examined from cultivated plants:

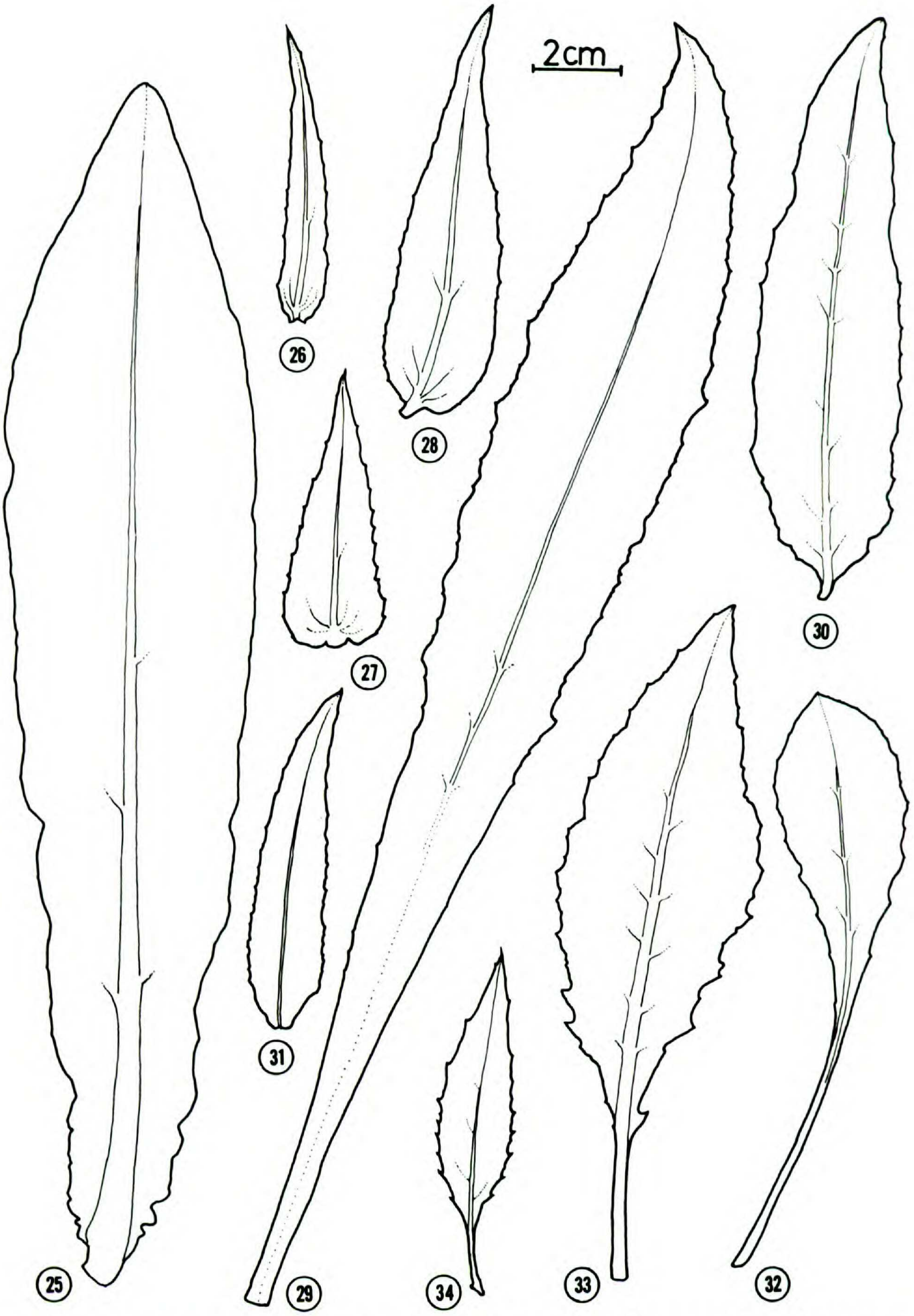
PERU. JUNÍN: Valley of Río Mantaro, Pachacayo, 3,650 m, *Santarius 2163**, *2180*, *2184* (DUSS, MO; *2163* also CTES, M). PUNO: Chimu, 8 km SE of Puno, *Santarius 2062** (DUSS).

BOLIVIA. COCHABAMBA: Liriuni near Cochabamba, *Diers in April 1959** (CTES, DUSS, MO). TARIJA: Road from Tarija to Villazón, km 33, 3,100 m, *Santarius 1946** (CTES, DUSS, M, MO).

Additional specimens examined:

ECUADOR. PINCHINCHA: Between Nono and Cotocollao, 3,100 m, *Asplund 20276* (LD, NY, R, S, UPS). W of Nono, 2,700 m, *Harling et al. 10253* (RSA).

PERU. ANCASH: Huaylas, Laguna Parón, 3,000 m, *Lopez 1878* (RSA). HUÁNUCO: Huacachi, near Muña, *Macbride 3884* (F, G, GH, US). Pillao, 2,700 m, *Woytowski in 1946* (F, MO, LIL, UC). LIMA: Río Blanco, 3,900 m, *Macbride & Featherstone 681* (F, GH). Rimac valley, 3,500 m, *N.N. in 1954* (RSA). Chicla near Huarochiri, 4,000 m, *Saunders 594* (BM). Oroya near Lima, *Kalenborn 41* (MO), *241* (GH, NY, US). AYACUCHO: Pampa de Chupas, *N.N. in 1969* (RSA). APURIMAC: Apurimac River near Cañas, 3,700 m, *Vargas 11044* (F, GH, K, UC). CUZCO: Cuzco, *Herrera in 1922* (SI); 3,350 m, *Balfour 102* (K). Paucartambo, Huaisampillo, 2,200 m, *Vargas 9976* (MO). Ollantaytambo, 3,000 m, *Cook & Gilbert 628* (US). PUNO: Puno, 4,000 m, *Soukup 109* (F). Carabaya, Antapampa, 4,180 m, *Vargas*



Figures 25–34. Leaves of South American taxa of *Oenothera* sect. *Oenothera* (continued).—25. Rosette leaf of *O. longituba* (Argentina, Catamarca, *Diers in 1959*).—26. Bract of *O. tarijensis* (Bolivia, Tarija, *Santarius 1924*).—27. Bract of *O. recurva* (Bolivia, Tarija, *Santarius 1941*).—28. Bract of *O. scabra* (Bolivia, Cochabamba, *Santarius 2003*).—29–31. Rosette leaf, cauline leaf, and bract of *O. longituba* (Argentina, Jujuy, *Fabris 5787*).—32–34. Rosette leaf, cauline leaf, and bract of *O. pedunculifolia* (Argentina, Tucumán, *Santarius 1745*).

7002 pro parte (LIL, POM). Azángaro, Tequena near Arapa, 3,900 m, *Aguilar 227* (USM). Capachica Peninsula of Titicaca Lake, 3,700 m, *Tutin 1009* (BM).

Bolivia. LA PAZ: La Paz, 3,800 m, *Buchtien 532* (GH, NY, UC, US). Tacacoma, *Cárdenas 5137* (US). Charasani near Muñecas, 2,700 m, *Cardenas 3844* (POM). Quime, 2,400 m, *Brooke 5396* (BM). Isla Titicaca, 3,840 m, *Buchtien 2921* (NY, US). Pongo, 3,650 m, *Tate 190* (NY). Titicaca, *Adolph & Bandelier in 1905* (NY). Vicinity of Sorata near Larecaja, 3,200 m, *Mandon 628* (P pro parte, S), *627* (BM, G, K, P, W pro parte). Gran Poder near Sorata, 3,050 m, *Brooke 6644* (BM). COCHABAMBA: 30 mi ENE Cochabamba, 3,750 m, *Brooke 5091* (BM). Choro above the Cocapata River, 3,050 m, *Brooke 6028* (BM, F, NY). ORURO: Caranga, *D'Orbigny in 1929* (P). POTOSÍ: Ingenio de Oro, 3,050 m, *Rusby 1976* (NY). CHUQUISACA: Cordillera de Sombreros, 3,100 m, *Troll 670* (M). TARIJA: La Aguada near Tarija, 3,300 m, *Balls 6112* (K, UC, US).

Argentina. JUJUY: Chorru Valley near Tilcara, 3,400 m, *Balls 6027* (K). Tilcara, Falda Grande, Cerro de Guairahuasi, 3,400 m, *Cabrera & Hernandez 14021* (LP). Sierra de Zenta, 4,000–4,500 m, *Budín 178* (GH, POM). Tumbaya, *Medinacely 9* (POM). Cerro Morado near Tumbaya, 3,300 m, *Fabris 6217* (BAA); *Cabrera 18306* (LP). Volcán near Tumbaya, 2,900 m, *Sleumer 3563* (LIL). Serrania de Calilegua, Tolditos, 2,600 m, *Fabris et al.* (LP). Serrania de Calilegua, Cerro Colorado, 2,700 m, *Fabris et al.* (LIL, LP). Purmamarca, Tascal near Tumbaya, 3,400 m, *Cabrera 15105* (LP). Puente del Diablo near Tres Cruces, 4,000 m, *Fabris & Marchionni 1746* (LP). Mina Aguilar near Tumahuaca, *Fernández 2003* (LP). Mina Aguilar, 4,400 m, *Sleumer 3383* (LIL). Mula Muerte, 2,700 m, *Castillón 119, 130* (LIL). SALTA: El Alisal near Cafayate, 2,800 m, *in 1914* (LIL). Santa Victoria, 2,385 m, *Sleumer 3780* (LIL). Lizoite near Sta. Victoria, 3,340 m, *Meyer & Bianchi in 1940* (LIL). TUCUMÁN: La Ciénaga, *Lorentz & Hieronymus 687, 689* (CORD, GOET); *Lillo 3707* (LIL). Cerro Negrito near Tafí, 3,500–3,600 m, *Sparre 6147* (LIL). La Queñua of the Sierra Calchaquies, 3,000 m, *Burkart 5366* (SI). Estancia Sta. Boza and Pto. La Cueva, 3,600 m, *Venturi 3165* (LIL, US). Malamala, 2,400 m, *Lillo 3443* (LIL). El Chorro near Trancas, 2,500–3,000 m, *Schreiter 1121* (LIL). CATAMARCA: Andalgala, *Jorgensen 1054* pro parte (LIL). LA RIOJA: Sierra de Famatima, slope of La Mesada, 3,500–3,700 m, *Kurtz 13946* (CORD). Between La Mesada and El Paso, 3,500–4,200 m, *Kurtz 14040* (CORD).

Early specimens from cultivated plants:

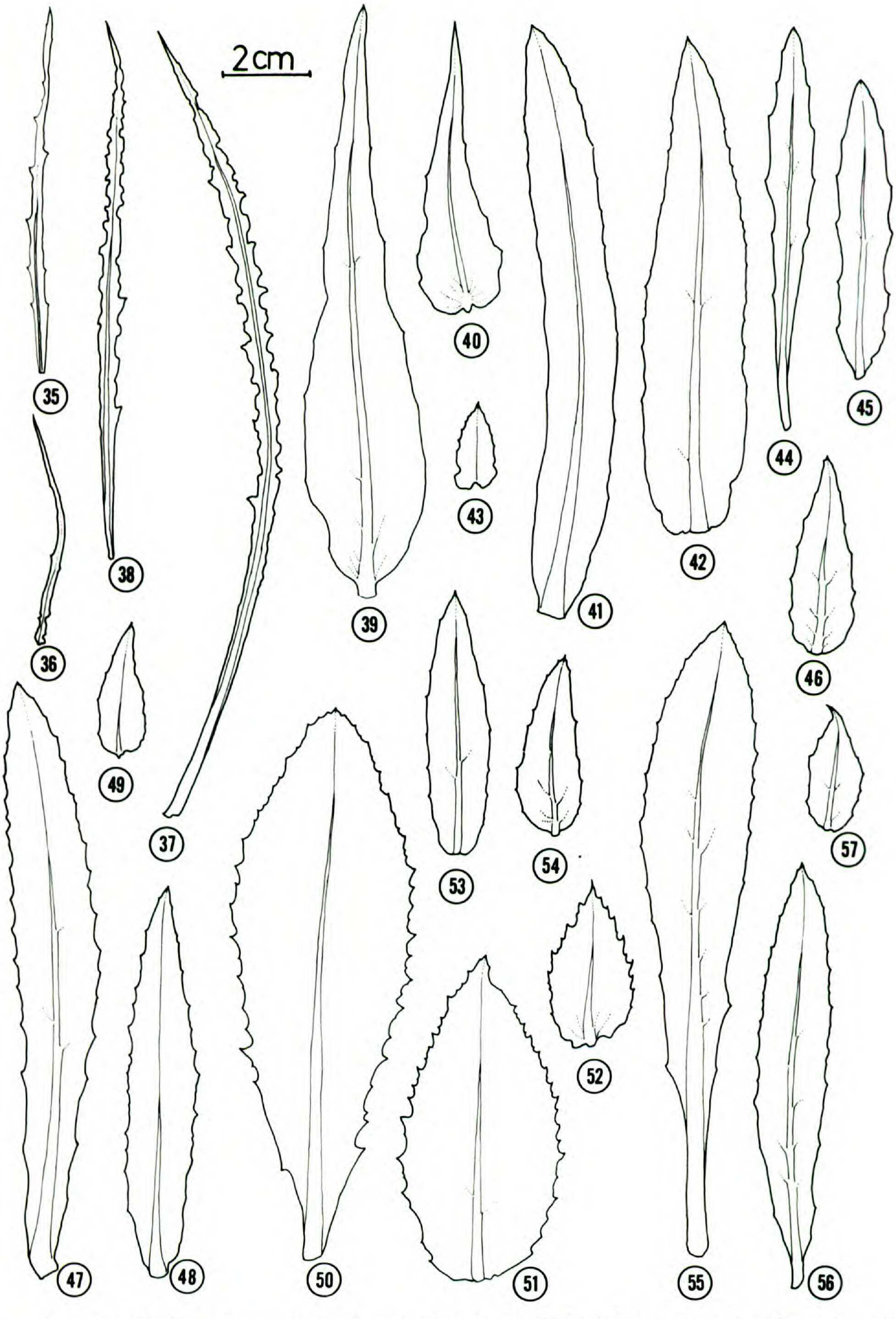
Ex herb. *J. Gay*, Jardin Vilmorin, Paris, 17 Aug. 1859, (K; as *O. versicolor*). Hort. Paris, Aug. 1865, *B. Verloti* (P; as *O. campylocarpa*).

The partial or pronounced red coloration of the veins and base of the petals and the predominantly strigillose pubescence are characteristic of *O. versicolor*. As might be expected from the very extensive range, there is a considerable and significant amount of variation, especially in the width of the leaves and their toothing. Plants intermediate with *O. lasiocarpa* occur in the provinces of Tucumán and Jujuy in Argentina. It is not known whether these are spontaneous hybrids or complex heterozygotes which characterize entire populations.

3. **Oenothera lasiocarpa** Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 143. 1874.—Figs. 105, 170.

O. campylocalyx sensu Munz, Physis 11: 286. 1933, pro parte.

Erect annual or biennial herb, forming a rosette, 1–3.5 dm tall. Plants unbranched or with a somewhat branched main stem and widely arcuate-ascending side branches arising from the rosette. Entire plant densely strigillose, especially in the region of the inflorescence, and also with erect long-villous pubescence. Rosette leaves narrowly oblanceolate to very narrowly elliptic, acute, gradually narrowed to the petiole, 6–12 cm long, 0.8–1.5 cm wide; cauline leaves mostly absent, since the plants generally bloom just above the rosette, but when present very narrowly elliptic, 5–10 cm long, with a short petiole or sessile; bracts narrowly lanceolate to oblanceolate, 3–8 cm long, 0.3–1.2 cm



FIGURES 35–57. Leaves of South American taxa of *Oenothera* sect. *Oenothera* (continued).—35–36. Cauline leaf and bract of *O. mendocinensis* (Argentina, Buenos Aires, *Santarius 421*).—37–38. Rosette leaf and cauline leaf of *O. odorata* (Argentina, Chubut, *Santarius 953*).—39–40. Cauline leaf and bract of *O. odorata* (Argentina, Río Negro, *Santarius 800*).—41–43. Rosette leaf, cauline leaf, and bract of *O. ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul,

wide, acute, acute to truncate at the base; leaves plane or undulate at the margins, irregularly serrate with coarse to slightly produced teeth. Inflorescence unbranched. Floral tube 1.5–2(–2.5) cm long. Buds oblong to narrowly ovate in outline, 1–2 cm long, 6–8 mm thick, often flushed with red; apices of the sepals erect, ca. 2 mm long. Petals very broadly obovate, 1.5–2 cm long, rounded or retuse, red near the base and along the veins. Anthers 4–6 mm long. Filaments 6–8 mm long. Style short, the stigma surrounded by the anthers at anthesis, or long, the stigma held above the anthers at anthesis, 2–3 cm long. Stigma lobes 3–5 mm long. Ovary 8–10 mm long. Capsule 1–2(–2.5) cm long, 5–8 mm thick, dark brown to very dark brown when ripe. Seeds 1–1.2 mm long, 0.6–0.8 mm thick, ± obscurely angled, dark brown. Self-compatible; self-pollinating or outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: November–April.

Type: Argentina, Prov. Catamarca, alpine meadows, Vayas Altas, Sierra de Belén, 2,950–3,650 m, mid-January 1872, *T. G. Lorentz 633* (GOET, holotype; CORD, isotype).

Distribution (Fig. 225): Andes of Argentina, in the provinces of Salta, Jujuy, Tucumán, Catamarca, La Rioja, and San Juan; 2,000–4,000 m elevation.

Specimens examined from cultivated plants:
ARGENTINA. TUCUMÁN: Tafi del Valle, 3,900 m, *Diers in 1959** (CTES, DUSS, M, MO).
Additional specimens examined:

ARGENTINA: JUJUY: Quebrada near Susques, *Cabrera 8760* (LP). Sierra de Zenta, 4,500 m, *Budin 7476* (LIL). Yavi Chico, 3,350 m, *Werner 286* (LP). Maimara, 2,230 m, *Budin 11790* (GH, LIL, POM, SI). Volcán, Loma del Tambo, 2,500–3,000 m, *Schreiter in 1924* (LIL). SALTA: Vicinity of Nevado del Castillo, *Lorentz & Hieronymus 47* (CORD, GOET). TUCUMÁN: Tafi, Cerro Muñoz, 3,000 m, *Lillo 7428, 4267* (LIL); *Castillon 177* (LIL). Río Blanco, 2,600 m, *Lillo 8868* (LIL). Lara near Tafi, 3,200 m, *Rodriguez 574* (GH). Quebrada del Barón, *Fabris 1371* (LP). Quebrada de la Hoyada, 1,500 m, *Schreiter 1875* (LIL). Calchaquies, 4,200 m, *Lillo 5516* (LIL); *Türpe in 1959* (LIL); *La Sota 2791* (LP). Peñas Azules, *Parodi 10971* (POM); *Burkart 5300* (SI); *Olea 8759* (LIL). La Queñoa, 2,800 m, *Schreiter 6995* (LIL). La Ciénaga, 2,800 m, *Sleumer 203* (LIL). Pojonal, 2,600 m, *Meyer & Vaca 23659* (LIL). Casa de Piedra, *Lillo 179* (LIL). Vicinity of Muñecas, *Castillon in 1905* (LIL). Chicligasta, Estancia Las Pavas, 3,000 m, *Venturi 4597* (BAB, LIL, SI). Trancas, Chorro, 3,400 m, *Venturi 8512* (US); *Schreiter 4790* (LIL). CATAMARCA: Andalgala, valley of Río Bolsón, 4,000 m, *Rohmeder in 1943* (LIL). Campo Grande, *Schickendantz 67* (CORD, GOET, SI); *Schickendantz 310* (CORD, GOET). Sierra de Ambato, between El Rodeo and Cerro Manchado, 2,900 m, *Hunziker 19196, 20998* (CORD); *Hunziker & Di Fulvio 19759, 19721* (CORD). Belén, slopes N of Portezuelo, 3,200–3,300 m, *Sleumer & Vervoorst 2606* (LIL, US). Tinogasta, La Tranca, *Castellanos 564* (POM). La Puntilla near Tinogasta, 2,700 m, *Hunziker 4356* (BAB). LA RIOJA: Sierra Famatima, La Vega de la Mesada, 3,650 m, *Kurtz 13928* (CORD, MO). Ciénaga de La Caldera, 3,600–3,650 m, *Kurtz 13935* (CORD). El Volcán, *Kurtz 14658* (CORD). Mina San Juan, 3,050–3,200 m, *Kurtz 13597, 13685* (CORD); Real Viejo, *Kurtz 14701* (CORD). Alto Blanco, *Castellanos 28-282* (POM). La

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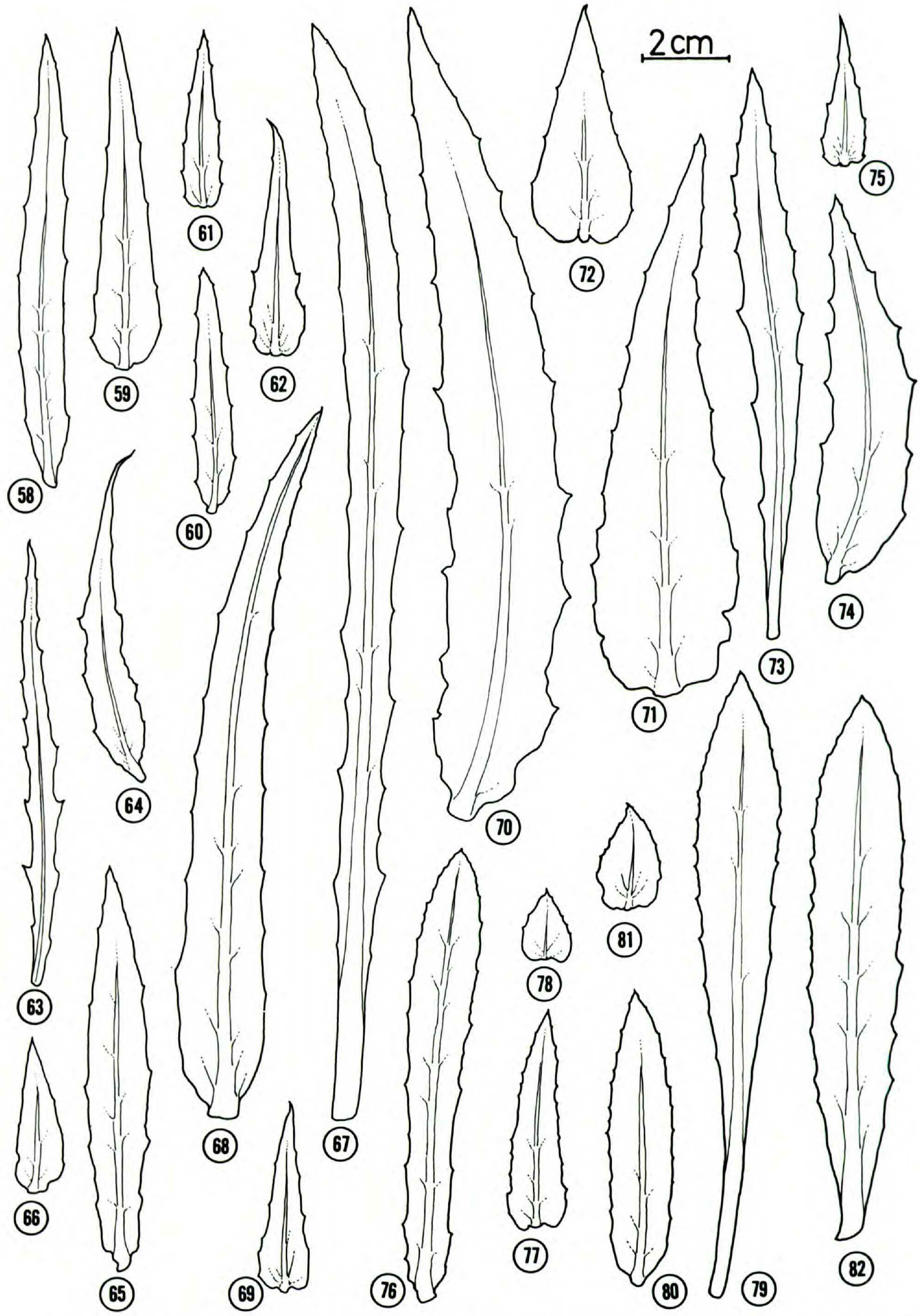
Hackbart in 1966).—44–46. Rosette leaf, cauline leaf, and bract of *O. indecora* subsp. *bonariensis* (Argentina, Corrientes, *Quarín & Schinini 1297*).—47–49. Rosette leaf, cauline leaf, and bract of *O. ravenii* subsp. *chilensis* (Chile, Cautín, *Stubbe in 1960*).—50–52. Rosette leaf, cauline leaf, and bract of *O. longiflora* subsp. *grandiflora* (Argentina, Corrientes, *Krapovickas & Cristóbal 11293*).—53–54. Cauline leaf and bract of *O. catharinensis* (Brazil, Santa Catarina, *Conrad & Dietrich 9*).—55–57. Rosette leaf, cauline leaf, and bract of *O. longiflora* subsp. *longiflora* (Uruguay, Colonia, *Santarius 73*).



FIGURES 58–82. Leaves of South American taxa of *Oenothera* sect. *Oenothera* (continued). —58–59. Cauline leaf and bract of *O. affinis* (Argentina, San Luis, *Conrad & Dietrich 139*). —60–61. Cauline leaf and bract of *O. mollissima* (Uruguay, Maldonado, *Santarius 161*).—62. Bract of *O. mollissima* (Uruguay, Maldonado, *Santarius 162*).—63–64. Cauline leaf and

Mejicana, 3,900 m, *Parodi 7896* (GH). Quebrada de Potrerillos, 3,800 m, *Krapovickas & Hunziker 5411, 5419* (BAB). Cueva de Perez, *Hieronymus & Niederlein 390* (CORD). Mina El Oro, *Hieronymus & Niederlein 414* (CORD). Lamadrid, Realitos, 3,800 m, *Rohmeder in 1941* (LIL). Real de los Neveros, 3,500 m (LIL-80298). Viejo, *Hossens 1422* (CORD). SAN JUAN: Cordillera del Salado, 3,800 m, *Spegazzini in 1957* (BAB). Cerro Tronador, *Spegazzini 212* pro parte (BAB).

Oenothera lasiocarpa is very closely related to *O. versicolor*, and the two are the only species of the series with pronounced red coloration of the petals. It can be separated from that species by its lower and more compact habit, erect long-villous pubescence, and dark green leaves; in *O. versicolor* the leaves are more grayish green. Small plants of *O. lasiocarpa* can also be confused with *O. nana*, but the latter does not develop a central shoot at all. Very small-leaved plants occur in *O. lasiocarpa* (e.g., *Budín 1170*), and some plants of *O. nana* growing in the area of *O. lasiocarpa* have broad leaves (*Lillo 5516, Rodríguez 1292, de la Sota 2711*) which, despite their occurrence as rosettes, resemble *O. lasiocarpa* closely. The first group of plants may be understood as occasional homozygous derivatives of *O. nana*. Similarly, the broad-leaved plants of *O. nana* may provide an indication that *O. lasiocarpa*, which is in all probability derived from *O. versicolor* in Argentina, may be involved in the origin of one of the chromosomal complexes of *O. nana*, which is always a complex heterozygote.

4. **Oenothera santarii** Dietrich, sp. nov.—Figs. 5, 20–22, 106, 171, 195.

O. odorata Jacq. var. *brachycarpa* Haumann, Anales Soc. Ci. Argent. 86: 292. 1919. LECTOTYPE: Argentina, Prov. Mendoza, Cordilleras Altas de Mendoza, Puente del Inca to Punta de Vacas, ca. 2,500 m, Jan. 1908, *L. Haumann* (BR).

Herba annua vel biennis, rosulata, 7–12 dm alta, simplex vel caulis principalis vix ramosa, ramis arcuatis e rosula ascendentibus. Herba sparse strigulosa, aliquantum in inflorescentiam densior, et pilis erectis sparsis praedita. Folia rosulae anguste oblanceolata, acuta, lamina in petiolum gradatim decrescens, 15–30 cm longa, 2.5–4 cm lata; folia caulina angustissime elliptica, acuta, basi acuta, 10–15 cm longa, 1–2.5 cm lata, brevipetiolata vel sessilia; bractea angustissime elliptica vel lanceolata, basi attenuata vel truncata, plerumque oblique ascendentia, sessilia, 5–8 cm longa, 1–1.5 cm lata, apicibus supremarum saepe in cochleam tortis; folia valde marginibus undulatis. Inflorescentia plerumque simplex. Tubus floralis 2–2.5 cm longus. Gemmae ambito lanceolatae, 2–2.5 cm longae, 5–8 mm crassae; apices sepalorum ca. 2 mm longi, erecti. Petala latissime obovata, lutea, 2–3 cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato, vel brevis, stigmate sub anthesi antheris circumdato. Ovarium 8–10 mm longum. Capsula 2–3 cm longa, 6–9 mm crassa, maturitate fusca. Semina ± obtuse angulata, 1.2–1.4 mm longa, 0.7–1 mm lata, fusca. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

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bract of *O. rivadaviae* (Argentina, Chubut, *Santarius 913*).—65–66. Cauline leaf and bract of *O. picensis* subsp. *cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—67–69. Rosette leaf, cauline leaf, and bract of *O. stricta* subsp. *altissima* (Argentina, Río Negro, *Santarius 798*).—70–72. Rosette leaf, cauline leaf, and bract of *O. stricta* subsp. *argentinae* (Argentina, Buenos Aires, *Santarius 346*).—73–75. Rosette leaf, cauline leaf, and bract of *O. bahia-blancae* (Argentina, Buenos Aires, *Santarius 455*).—76–78. Rosette leaf, cauline leaf, and bract of *O. parodiana* subsp. *parodiana* (Argentina, Córdoba, *Conrad & Dietrich 98*).—79–81. Rosette leaf, cauline leaf, and bract of *O. parodiana* subsp. *parodiana* (Argentina, Córdoba, *Conrad & Dietrich 162*).—82. Rosette leaf of *O. parodiana* subsp. *parodiana* (Argentina, Córdoba, *Conrad & Dietrich 122*).

Erect annual or biennial herbs, forming a rosette, 7–12 dm tall. Plants unbranched or with a scarcely branched main stem and widely arcuate-ascending side branches arising from the rosette. Plant sparsely strigillose, somewhat more densely so in the inflorescence, also with sparse, erect, villous pubescence. Rosette leaves narrowly oblanceolate, acute, gradually narrowed to the petiole, 15–30 cm long, 2.5–4 cm wide; cauline leaves very narrowly elliptic, acute, acute at the base, 10–15 cm long, 1–2.5 cm wide, with a short petiole or sessile; bracts very narrowly elliptic to lanceolate, acute, acute to truncate at the base, usually obliquely ascending, sessile, 5–8 cm long, 1–1.5 cm wide, the tips of the uppermost ones often slightly spirally twisted; all leaves plane to strongly undulate at the margins and irregularly toothed. Inflorescence usually unbranched. Floral tube 2–2.5 cm long. Buds lanceolate in outline, 2–2.5 cm long, 5–8 mm thick; apices of the sepals erect, ca. 2 mm long. Petals very broadly obovate, yellow, 2–3 cm long. Anthers 9–11 mm long. Filaments 18–20 mm long. Style long, the stigma elevated above the anthers at anthesis, or short, the anthers shedding pollen directly on the stigma at anthesis, 3–5.5 cm long. Stigma lobes 3–5 mm long. Ovary 8–10 mm long. Capsule 2–3 cm long, 6–9 mm thick, brown when ripe. Seeds 1.2–1.4 mm long, 0.7–1 mm thick, more or less obtusely angular, brown. Self-compatible. Gametic chromosome number, $n = 7$ (7 bivalents* or small rings at meiotic metaphase I). Flowering time: November–March.

Type: Grown from seeds and cultivated at the Botanical Garden of Düsseldorf, Germany, 15 Aug. 1972. Source: Argentina, Prov. Mendoza, Cordillera de Los Andes, on stony places at Ruta 7, ca. 150 m E of Arroyo Santa Maria, ca. 6 km E of Puente del Inca, 2,750 m, 25 Feb. 1968, *K. A. Santarius 1430* (MO-2155403, holotype; CTES, DUSS, M, isotypes).

Distribution (Figs. 225, 241): Andes of Argentina west of Mendoza, and one locality in the province of San Juan, as well as in the Sierra de Córdoba and the Sierra de Comechingones (provinces of Córdoba and San Luis), 1,800–3,000 m elevation.

Specimens examined from cultivated plants:

ARGENTINA: MENDOZA: Cordillera de los Andes, Puente del Inca, 2,700–2,750 m, *Santarius 1405*, 1417*, 1430*, 1436*, 1443*, 1444*, 1455** (DUSS; *1430, 1435, 1436, 1455* also M; *1430, 1444* also MO). Punta de Vacas, 2,450 m, *Santarius 1492, 1500** (DUSS; *1492* also MO). Polvaredas, 2,450 m, *Santarius 1535* (DUSS, MO). SAN LUIS: Sierra de Comechingones, El Rincón, 1,500 m, *Conrad & Dietrich 152* (ring of 4 and 5 bivalents, ring of 6 and 4 bivalents) (DUSS).

Additional specimens examined:

ARGENTINA. SAN JUAN: Jáchal, Río Blanco near Punilla, *Hossens 169* (CORD). MENDOZA: Punta de Vacas, *Spegazzini in 1901* (POM), *90729, 90730* (BAB); 2,700 m, *King 695* (BM). Puente del Inca, 2,800 m, *Boelcke 9840* (BAA, BAB, MO, SI); *Spegazzini 24213* (BAB); *Wall in 1946* (S); 3,000 m, *Sparre 1644* (S); *King 430* (BAB); 2,700 m, *Ruiz Leal 6554* (LIL, Leal); *Yepes 26-762* (POM); *Gosse in 1897* (K, NY); *Malme 2858* (S); *Dawson 60* (SI). Between Puente del Inca and Las Polvaredas, *Moreau 12667* (BA). Las Heras, Arroyo Sta. Maria, 2,400 m, *Calastremé 72031* (BAB, CORD). Quebrada Sta. Maria, 2,800 m, *Hunziker 3246* (BAB, CORD). Luján, Los Vallecitos, *Ruiz Leal 22565* (Leal); 2,700 m, *Leal 13404* (Leal). Cancha de Esqui, 3,000 m, *Cuezzo & Say 2540* (LIL). Tunuyán, Quebrada Cap. Lemos, 2,300 m, *Palacios & Cuezzo 4459* (LIL). Malalhue, Tronquimalal, *Castellanos 15492* (US). CORDOBA: Sierra Grande, Valle de Los Reartes, *Castellanos 1556* (POM).

Cuesta da las Calvas, 1,800 m, *Hunziker 9682* (CORD, RSA). Pampa de Achala, near Copina, 1,900 m, *Hunziker 11912* (RSA). Sierra Achala, Cerro Los Gigantes, 2,400 m, *Doering 15659, 15647* (CORD). Copina, *Hieronymus 634* (GOET). San Javier, Loma Bela, 1,500 m, *Hunziker 8293* (CORD). Peak of the Champaquí, *Hunziker 9040* (CORD). SAN LUIS: Sierra de Comechingones, El Rincón, *Hunziker 11782* (RSA), *11789* (CORD, MO). Cerro de Piedra, *Vignati 15* (SI). Monigote, *Gerth in 1914* (L).

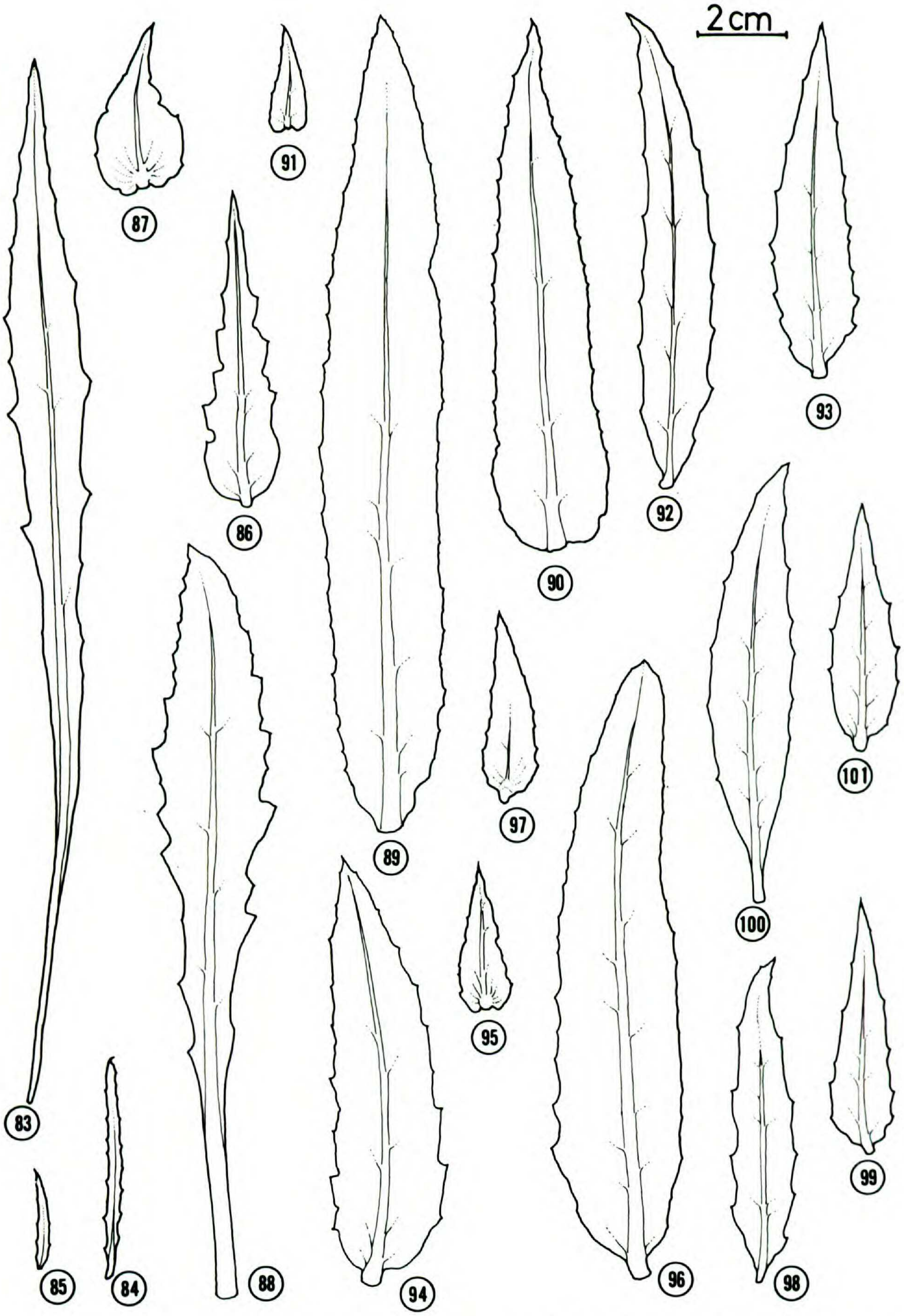
This new species is dedicated to Kurt A. Santarius (1933–), who contributed so much to this study with his extensive collections of seeds from throughout South America. It is the southernmost of the series. The very local and widely separated stations that make up its distribution are suggestive of a wider range to the north in the past. The *santarii*-complex is, however, the most widespread of all genomes of the group. *Oenothera magellanica* (*santarii–odorata*) is found throughout Argentina from Mendoza southward and southeastward to south of Punta Arenas in southernmost Patagonia; northward it radiates to the province of San Juan. As *Oenothera villaricae* (*santarii–ravenii*) the genome occurs in central Chile.

5. **Oenothera longituba** Dietrich, sp. nov.—FIGS. 25, 29–31, 107–108, 172, 196–197.

O. campylocalyx sensu Munz, Physis 11: 286. 1933, pro parte.

Herba erecta verosimiliter biennis, rosulata, 5–10 dm alta, simplex vel caulis principalis sparse ramosa et ramis lato-arcuate e rosula ascendentibus. Herba dense ad sparse strigulosam et ubique pilis longis erectis praedita, in inflorescentiam densiore pubescens. Folia rosulae anguste elliptica vel oblanceolata, acuta, lamina in petiolum brevem gradatim decrescens vel sessili, 17–35 cm longa, 2–6 cm lata; folia caulina elliptica vel ovata, acuta, basi acuta vel truncata, sessilia, 8–17 cm longa, 1.5–4 cm lata; bractea lanceolata vel ovata, acuta, basi rotundata vel subcordata, sessilia, 5–10 cm longa, 1–4 cm lata, sub anthesi maturitateque plerumque ad caulem perpendicularia. Inflorescentia plerumque simplex. Tubus floralis (5–) 7–10 cm longus. Gemmae ambito lanceolatae, 2.5–3.5 cm longae, 7–9 mm crassae, flavovirides, saepe rubrae, junctura sepalorum tubo florali anguste rubro-fasciatae; apices sepalorum 2–4 mm longi, erecti vel divergentes. Petala latissime obovata, rotundata vel retusa, 2–4 cm longa. Stylus longus, stigmata anthesi supra antheras elevata. Ovarium ca. 10 mm longum. Capsula 1.5–2.5 cm longa, 5–9 mm crassa, maturitate brunnea. Semina ± obtuse angulata, 1–1.5 mm longa, 0.5–0.6 mm lata, nigra. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Erect probably biennial herb, forming a rosette, 5–10 dm tall. Plants unbranched or with a scarcely branched main stem and widely arcuate-ascending side branches arising from the rosette. Plants densely or sparsely strigillose and with an admixture of erect villous pubescence throughout, most densely pubescent in the inflorescence. Rosette leaves narrowly elliptic or oblanceolate, acute, gradually narrowed to a short petiole or sessile, 17–35 cm long, 2–6 cm wide; cauline leaves elliptic to ovate, acute, acute to truncate at the base, sessile, 8–17 cm long, 1.5–4 cm wide; bracts lanceolate to ovate, acute, rounded to subcordate at the base, sessile, 5–10 cm long, 1–4 cm wide, in flower and fruit mostly spreading at right angles to the main stem; all leaves plane to undulate at the margins and irregularly toothed. Inflorescence usually unbranched. Floral tube (5–)7–10 cm long. Buds lanceolate in outline, 2.5–3.5 cm long, 7–9 mm thick, yellowish green, often flushed with red, narrowly red-striped at the junction of the sepals with the floral tube; apices of the sepals erect or spread-



FIGURES 83–101. Leaves of South American taxa of *Oenothera* sect. *Oenothera* (continued).—83. Rosette leaf of *O. magellanica* (Argentina, Chubut, *Santarius 1393*).—84–85. Cauline leaf and bract of *O. punae* (Argentina, Tucumán, *Krapovickas 21851*).—86–87. Cauline leaf and bract of *O. grisea* (Chile, Valparaíso, *Constance in 1965*).—88. Rosette leaf of *O. villaricae* (Chile, Cautín, *Stubbe in 1960*).—89–91. Rosette leaf, cauline leaf, and bract of

ing, 2–4 mm long. Petals very broadly obovate, rounded to retuse, 2–4 cm long. Anthers 8–12 mm long. Filaments 20–30 mm long. Style long, the stigma held above the anthers at anthesis, (6–)8–12 cm long. Stigma lobes 6–10 mm long. Ovary ca. 10 mm long. Capsule 1.5–2.5 mm long, 5–9 mm thick, dark brown when ripe. Seeds 1–1.5 mm long, 0.5–0.6 mm thick, black, ± obtusely angled. Self-compatible but outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 15 Aug. 1972. Source: Argentina, Prov. Catamarca, near La Banderita at road from Andalgala to Concepción, 1,800 m, 11 Feb. 1959, *L. Diers* (MO-2155402, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 227): Andes of Argentina and their foothills in the provinces of Jujuy, Salta, Tucumán, Catamarca, and La Rioja, 900–3,000 m elevation.

Specimens examined from cultivated plants:

ARGENTINA. JUJUY: Sierra Calilegua, Cerro Colorado, 2,900 m, *Fabris 5787** (CTES, DUSS, M, MO). TUCUMÁN: Valle de Tafí, 5 km N of Tafí del Valle, 2,000–2,250 m, *Santarius 1736**, *1737** (DUSS; *1736* also CTES, M, MO). CATAMARCA: Near La Banderita at road from Andalgala to Concepción, 1800 m, *Diers in 1959** (DUSS, M, MO).

Additional specimens examined:

ARGENTINA. JUJUY: Santa Barbara, Cerro El Centinela, *Legname & Cuezzo 5103* (LP); 2,650 m, *Fabris 5133* (LP, RSA); *Legname & Cuezzo 5199* (LIL). Valle Grande, Serrania de Calilegua, *Fabris et al. 5880* (LIL). Serrania de Calilegua, Cerro Hermosa, 2,700 m, *Fabris et al. 5391* (CTES, LP), 2,800 m, *5830* (LP). SALTA: Rosario de Lerma, Campo Tuijano, 1,500 m, *Venturi 8098* (GH, SI). La Viña, Coronel Moldes, Río Chaña Pampa, 1,200 m, *Hunziker 1068* (POM, US). TUCUMÁN: Tafí, Taficillo, 1,800 m, *Venturi 5986* (LIL, US). Yerba Buena, 750 m, *Venturi 243* (LIL, SI). San Javier, 900 m, *Venturi 243* (US); *Lillo 136* (P). Río Angostura, 1,800 m, *Sparre 1356* (S). Villa Nougués, 1,000 m, *Munz 15463* (NY, US); *Schreiter 706* (F, LIL). Infiernillo, 2,450 m, *Meyer & Vaca 23669* (LIL). Duraznillo, *Rocha 2499* (LIL). San Javier, *Rocha 870* (LIL). Tafí del Valle, 3,000 m, *Sleumer 258* (LIL). Siambón, ca. 900 m, *Munz 15470* (POM); *Lorentz 306* (CORD, GOET). Aconquija, Esquina, 1,560 m, *Lillo 1572* (LIL). Laguna del Tesoro, 2,800 m, *Türpe in 1958* (LIL). Chicligasta, Est. Los Pavos to Pto. El Bayo, 3,200 m, *Venturi 3283* (LIL), 3,000 m, *4597* (US). CATAMARCA: Andalgala, El Clavillo, 1,900 m, *Jörgensen 1560* LIL, SI, US). Andalgala, Río Vallecito, 2,500 m, *Rohmeder in 1942* (LIL). Yacutula near Belén, *Schickendantz 114* (CORD). LA RIOJA: Sierra de Famatima, La Hoyada, 2,500 m, *Kurtz 15042, 15044* (CORD, MO). Sierra Velasco, Yacuchi, *Kurtz 15367* (CORD). Sarmiento, Juntas del Bonete and Ciénaga Grande, *Krapovickas & Hunziker 5909* (BAB).

Oenothera longituba is unmistakable because of its sturdy rosette and the long floral tubes that elevate the mature buds and flowers above the apex of the stem. Its genome has been involved in the origin of several complex structural heterozygotes, namely *O. tarijensis* (*versicolor–longituba*), *O. recurva* (*longituba–scabra*); it is also present in the predominantly Peruvian *O. weberbaueri*, so that this genome or at least one very similar must have been playing an active

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O. hechtii (Argentina, Tucumán, *Hecht 1964-81*).—92–93. Cauline leaf and bract of *O. acuticarpa* (Argentina, Tucumán, *Göpel in 1961*).—94–95. Cauline leaf and bract of *O. cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—96–97. Cauline leaf and bract of *O. siambonensis* (Argentina, Tucumán, *Hecht 1964-84*).—98–99. Cauline leaf and bract of *O. tucumanensis* (Argentina, Tucumán, *Santarius 1657*).—100–101. Cauline leaf and bract of *O. brevipetala* (Bolivia, Cochabamba, *Santarius 1972*).

role at least as far as Peru in the past. The genome of *O. longituba* has also entered into combinations with *O. affinis* and *O. ravenii* of series *Allochroa*, and from these combinations *O. elongata* and *O. hechtii*, which belong to series *Clelandia*, have arisen.

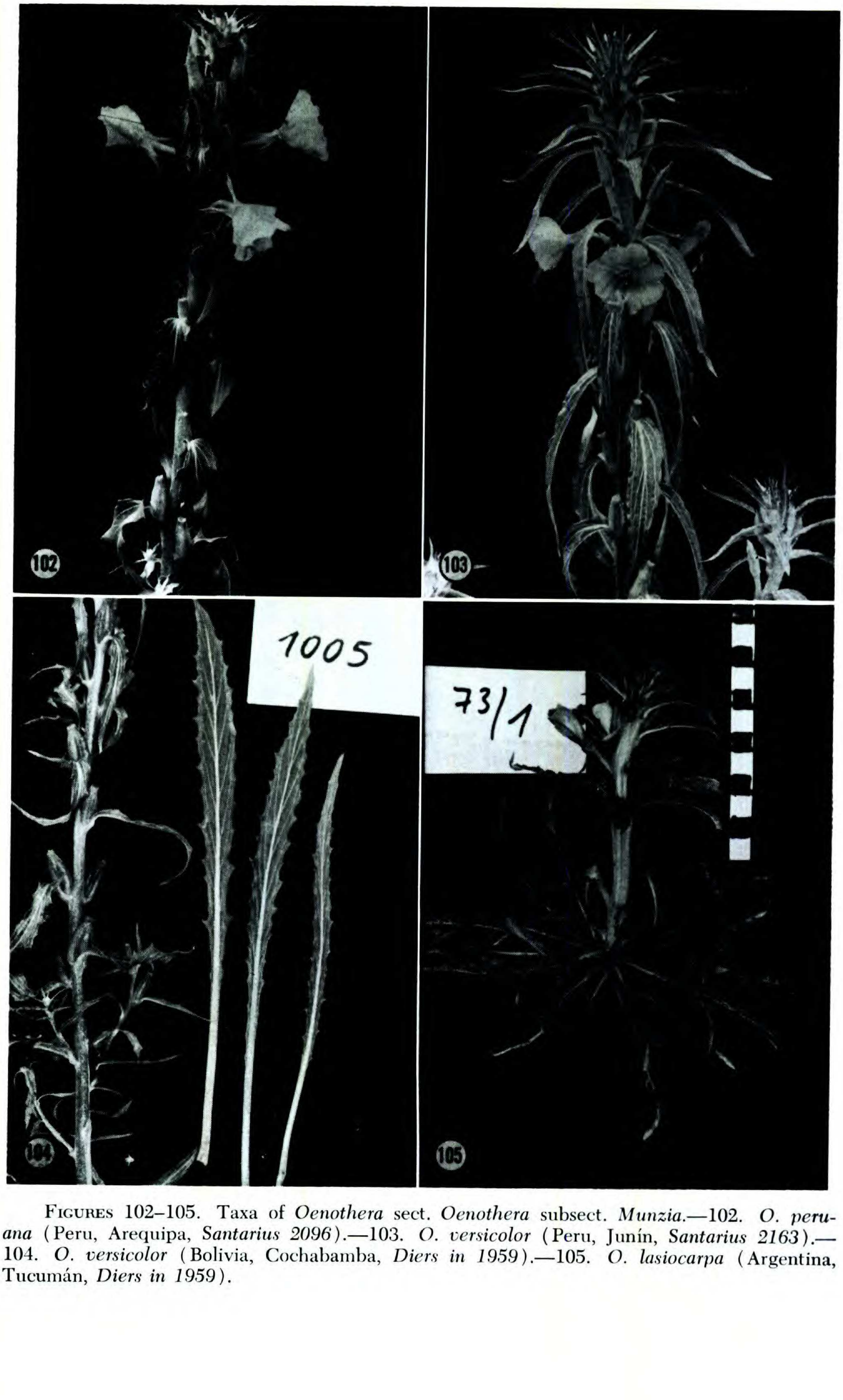
On the basis of the striking similarity in habit with *O. longiflora* and *O. ravenii*, it can be concluded that these species may have originated from an ancestor that resembled *O. longituba*.

6. **Oenothera tafiensis** Dietrich, sp. nov.—FIGS. 17–19, 23, 109–110.

Herba erecta annua vel biennis, rosulata, 4–10 dm alta, simplex vel caulis principalis crassus vel gracilis et ramis arcuate e rosula ascendentibus. Herba dense vel densissime strigulosa, etiam in inflorescentiam appresse villosa. Folia rosulae anguste elliptica vel anguste oblanceolata, acuta, lamina in petiolum gradatim vel ± abrupte decrescens, 15–20 cm longa, 1.5–2.5 cm lata; folia caulina anguste elliptica vel anguste lanceolata, acuta, basi anguste cuneata vel anguste lanceolata, 5–13 cm longa, 1–2 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi acuta vel truncata, sessilia, 5–8 cm longa, 1–2 cm lata; folia irregulariter obtuseque serrata. Inflorescentia plerumque simplex. Tubus floralis 2.5–5.5 cm longus. Gemmae ambito oblongae vel lanceolatae, 1.5–3 cm longae, 5–7 mm crassae, cinereo-virides vel flavescentes, junctura sepalorum tubo florali anguste rubro-fasciatae; apices sepalorum ca. 2 mm longi, erecti vel divergentes. Petala latissime obovata, retusa, 1.5–4 cm longa. Stylus brevis, stigmata anthesi antheribus circumdato. Ovarium 8–10 mm longum. Capsula 1.5–3 cm longa, 5–9 mm crassa, brunnea punctibus rubro-fuscis maculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Erect annual or biennial herbs, forming a rosette, 4–10 dm tall. Plants unbranched or with a very thick to slender main stem and arcuately ascending side branches arising from the rosette. Entire plant densely to very densely strigillose with an admixture of appressed long-villous pubescence in the inflorescence. Rosette leaves narrowly elliptic to narrowly oblanceolate, acute, gradually or ± abruptly narrowed to the petiole, 15–20 cm long, 1.5–2.5 cm wide; cauline leaves narrowly elliptic to narrowly lanceolate, acute, narrowly cuneate to narrowly lanceolate at the base, 5–13 cm long, 1–2 cm wide; bracts narrowly lanceolate to lanceolate, acute, acute to truncate at the base, sessile, 5–8 cm long, 1–2 cm wide; leaves usually plane at the margins, irregularly and bluntly serrate. Inflorescence usually unbranched. Floral tube 2.5–5.5 cm long. Buds oblong to lanceolate in outline, 1.5–3 cm long, 5–7 mm thick, gray green or yellowish, red striped at the junction of the sepals with the floral tube; apices of the sepals erect or spreading, ca. 2 mm long. Petals very broadly obovate, retuse, 1.5–4 cm long. Anthers 6–15 mm long. Filaments 12–30 mm long. Style short, the anthers usually shedding pollen directly on the stigma at anthesis, 3.5–8.5 cm long. Stigma lobes 3–8 mm long. Ovary 8–10 mm long. Capsule 1.5–3 cm long, 6–8 mm thick, dark gray brown when ripe. Seeds elliptic, 1–1.2 mm long, 0.5–0.6 mm thick, brown, flecked with dark reddish brown. Modally self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: northern area, December–May; southern area, December–March.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 25 July 1972. Source: Argentina, Prov. Tucumán, bed of Río Angostura from Tafí del Valle upstream for ca. 5 km N, mostly gravel, ca. 2,000–



FIGURES 102–105. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—102. *O. peruana* (Peru, Arequipa, *Santarius 2096*).—103. *O. versicolor* (Peru, Junín, *Santarius 2163*).—104. *O. versicolor* (Bolivia, Cochabamba, *Diers in 1959*).—105. *O. lasiocarpa* (Argentina, Tucumán, *Diers in 1959*).

2,250 m, 10 Mar. 1968, *K. A. Santarius 1735* (MO-2155400, holotype; DUSS, M, MO, isotypes).

Distribution (Figs. 228–229): Andes and Sierra de Córdoba of Argentina in the provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, and Córdoba, 1,500–3,000 m elevation.

Oenothera tafiensis can be separated from the very similar *O. scabra* by its entirely appressed pubescence.

KEY TO THE SUBSPECIES

1. Buds 2–3 cm long, lanceolate in outline; apices of the sepals erect; petals 2–4 cm long .... 6a. subsp. *tafiensis*

1′. Buds 1–1.5 cm long, oblong in outline; apices of the sepals divergent; petals 1.5–2 cm long .... 6b. subsp. *parviflora*

6a. **Oenothera tafiensis** subsp. **tafiensis**.—FIGS. 17–19, 109.

O. campylocalyx sensu Munz, Physis 11: 289. 1933, pro parte.
O. campylocalyx sensu Descole, Gen. Sp. Pl. Argent. 2: *tab. 164.* 1944.

Main stem unbranched or branched and with arcuate-ascending side branches arising from the rosette. Rosette leaves narrowly lanceolate, gradually narrowed to the petiole. Floral tube 2.5–5 cm long. Buds lanceolate in outline, 2–3 cm long, gray green; apices of the sepals erect. Petals 2–4 cm long. Anthers 10–15 mm long. Filaments 15–30 mm long. Style 3.5–8.5 cm long. Stigma lobes 5–8 mm long.

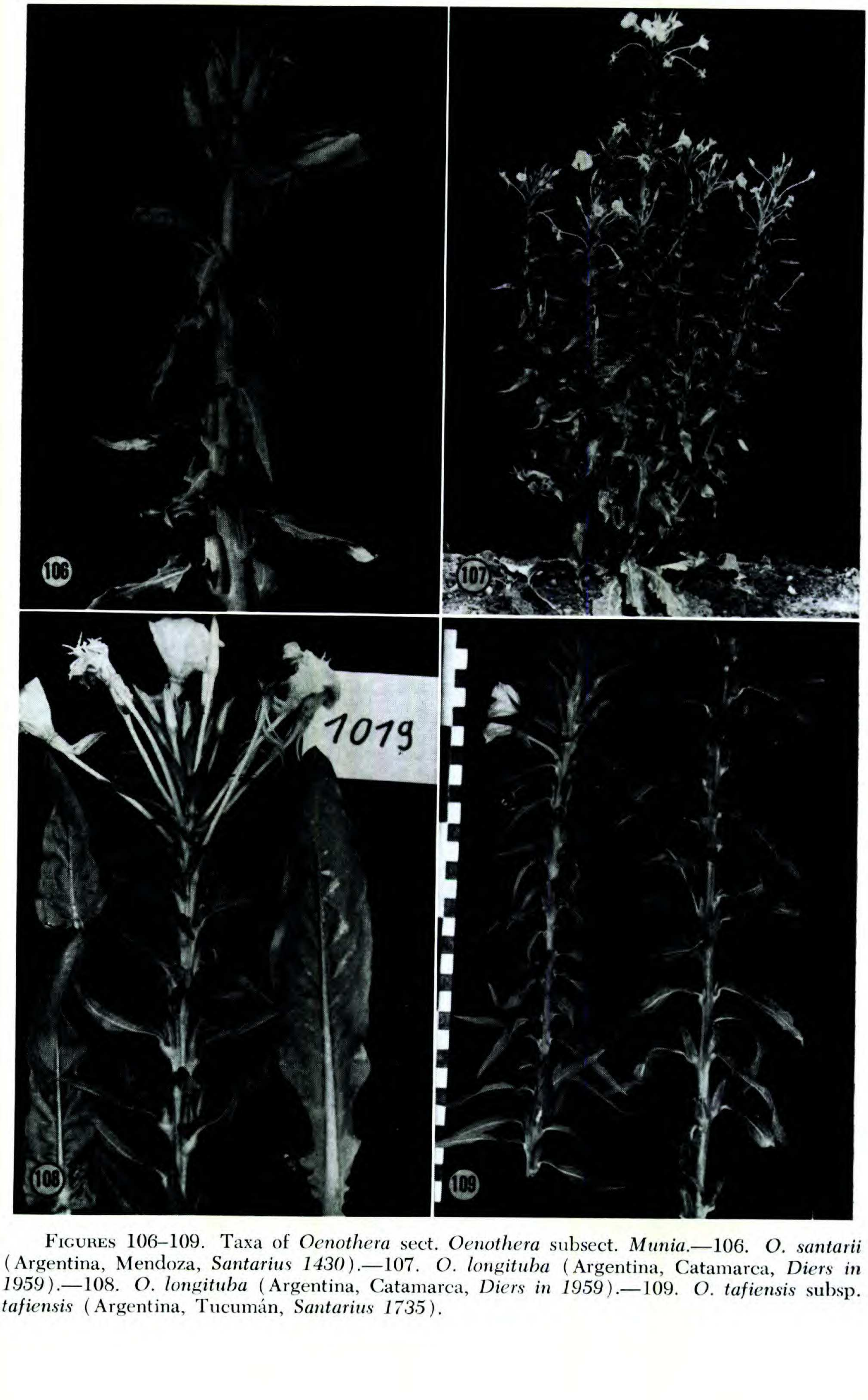
Distribution (Fig. 228): As in the species.

Specimen examined from cultivated plants:

ARGENTINA. TUCUMÁN: Bed of Río Angostura, 5 km N of Tafí del Valle, 2,000–2,250 m, *Santarius 1733*, *1735**, *1739**, *1741** (DUSS; *1735* also M; *1733*, *1735* also MO).

Additional specimens examined:

ARGENTINA. JUJUY: Termas de Reyes, *Hunziker 26196* (RSA); *Romero in 1947* (LIL). Laguna Yala, 2,100 m, *Romero in 1947* (LIL); *O'Donnell 4832* (LIL); *Cabrera et al. 21273* (LP). Tumbaya, Volcán, Chilcayo, *Cabrera 18207* (LP). Volcán, *Romero in 1947* (LIL). Est. Volcán, 2,100 m, *Castillon 322* (LIL). Valle Grande, Serrania de Calilegua, Mesias, *Fabris et al. 5858* (LIL). Guachipas, between Pampa Grande and El Lajar, *Meyer 21940* (LIL). SALTA: Cachi, peak of Obispo, *Romero in 1947* (LIL). San Fernando to the peak of Obispo, *Meyer 12481* (LIL). Cachi, Adentro, *Romero in 1947* (LIL). El Alisal, Cerro de Capán, 2,800 m, *Rodriguez 1298* (LIL, POM, SI). Sierra de la Candelaria, 2,200 m, *Venturi 3811* (BAB, LIL, SI, US). Slope of Unquillo near Candelaria, 2,000 m, *Schreiter 9435* (LIL). San Pedro near Truya, 3,000 m, *Petersen & Hjerting 224* (C, LIL). TUCUMÁN: Anfama, *Monetti 288* (BAB). Valle de Tafí, *Bruch in 1908* (LP, NY, RSA); *Türpe in 1959* (LIL). La Escorzonera, 2,000 m, *Lourteig 480*, *496* (LIL). La Quebradita, 2,000 m, *Lourteig 484* (LIL). Tafí, Valdas del Cerro, 2,000–3,000 m, *Lourteig 528* (LIL). Quebrada de Mastil, 2,200 m, *De La Sota 155* (LIL). La Ciénaga, *Descole 1529* (LIL); *Lillo 4008*, *4020* (LIL); *Lorentz & Hieronymus* 688 (GOET). Tafí, *Dinelli 597* (BAB). Sierra del Cajón, La Silla, 3,000 m, *Venturi 4504* (LIL). Tafí, 2,000 m, *Sparre 5648* (LIL). Chaquivil, *Olea 180* (LIL). Taficillo, *Olea in 1945* (LIL). Tafí, Río Churqui, 2,000 m, *Schreiter 1275* (LIL). Cerro San Javier, 1,200 m, *Lillo 367* (LIL). Matorrales, 2,000 m, *Lillo 3039* (LIL). Anfama, 2,500 m, *Lillo 3985* (GH, LIL, POM, UC). Tafí, *Lillo 3547*, *3102*, *4109*, *4287* (LIL), *4311* (F, LIL), *7452* (F, LIL, POM, US). Río Blanco, 2,600 m, *Lillo 4266* (LIL). Río del Churqui, 2,010 m, *Lillo 7511* (LIL). Slope of Malamala, 2,400 m, *Lillo 3417* (LIL), 2,800 m, *4357* (LIL). Siambón, El Matadero, 1,100 m, *Lillo 1770* (LIL). Siambón, 2,100 m, *Lillo 1772* (LIL). Chicligasta, Est. Las Pavas, 2,600 m, *Lillo 4135* (LIL). Chicligasta, between La Cascada and



FIGURES 106–109. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munia*.—106. *O. santarii* (Argentina, Mendoza, *Santarius 1430*).—107. *O. longituba* (Argentina, Catamarca, *Diers in 1959*).—108. *O. longituba* (Argentina, Catamarca, *Diers in 1959*).—109. *O. tafiensis* subsp. *tafiensis* (Argentina, Tucumán, *Santarius 1735*).

Las Cuevas, 3,000 m, *Meyer 14957* (LIL, RSA). Burroyacú, Cerro del Campo, 2,500 m, *Bailletti 8* (GH, LIL); *Stuckert 22000* (CORD). Aconquija, 1,560 m, *in 1890* (LIL). Trancas, 1,950 m, *N.N. 276* (LIL). CATAMARCA: Andalgala, *Jörgensen 1054* pro parte (US), *1058* pro parte (GH, MO, SI). El Suncho, 2,500 m, *Jörgensen 1058* (US). Andalgala, "Las Mesadas," 1,650 m, *Pedersen & Hjerting in 1949* (C); *Brücher in 1949* (LD). Río Vallecito, 2,500 m, *Rohmeder in 1942* (LIL). Río Potrero, 2,600 m, *Rohmeder in 1942* (LIL). Los Quenoales, Mesada de las Rosas, 2,500–2,700 m, *Sleumer 2241* (LIL). Yunka Suma, *Meyer 14718* (LIL). Santa Maria, Sierra de Anconquija, 3,100 m, *Peirano in 1933* (LIL). Cuesta Muschaca, *Schickendantz in 1876* (CORD). El Rodeo, *Mawecin 26* (CORD). Pomán, Cerro Manchado, 2,500–2,750 m, *Hunziker & Ariza 20507* (CORD). LA RIOJA: Sierra Velazco, Yacuchi, 2,100 m, *Kurtz 15384* (CORD). Velazco, 2,200 m, *Soriano 1003* (SI). Sierra de Famatima, La Mesada, 3,500 m, *Kurtz 13837* (CORD). CÓRDOBA: Valle de los Reartes, *Hicken 94* (SI); *Castellanos in 1920* (LIL), *94* (SI). Est. San Bernardo, 1,400 m, *Hunziker 12056* (CORD), *12006* (RSA). Colón, Salsipuedes, *Dawson 84* (NY). Valle de Punilla, Capilla del Monte, road to Huertas Malas, *Hossens 416* (CORD).

At least in cultivation, the first five species listed all form a heavy rosette first. From this rosette subsequently arises the main shoot and several side branches. *Oenothera tafiensis* subsp. *tafiensis* is different in this respect, since the rosette often sprouts near the base of the main shoot, without forming branches itself. Since the rosette leaves, coming in contact with the ground, soon rot, the plant soon assumes the habit of the early-bolting *O. scabra*. In addition, the flecked seeds suggest that *O. tafiensis* occupies a position intermediate between the rosette-forming and the early-bolting species, which are probably to be regarded as derivative species in view of the fact that they are obligate annuals.

6b. **Oenothera tafiensis** subsp. **parviflora** Dietrich, subsp. nov.—FIGS. 23, 110.

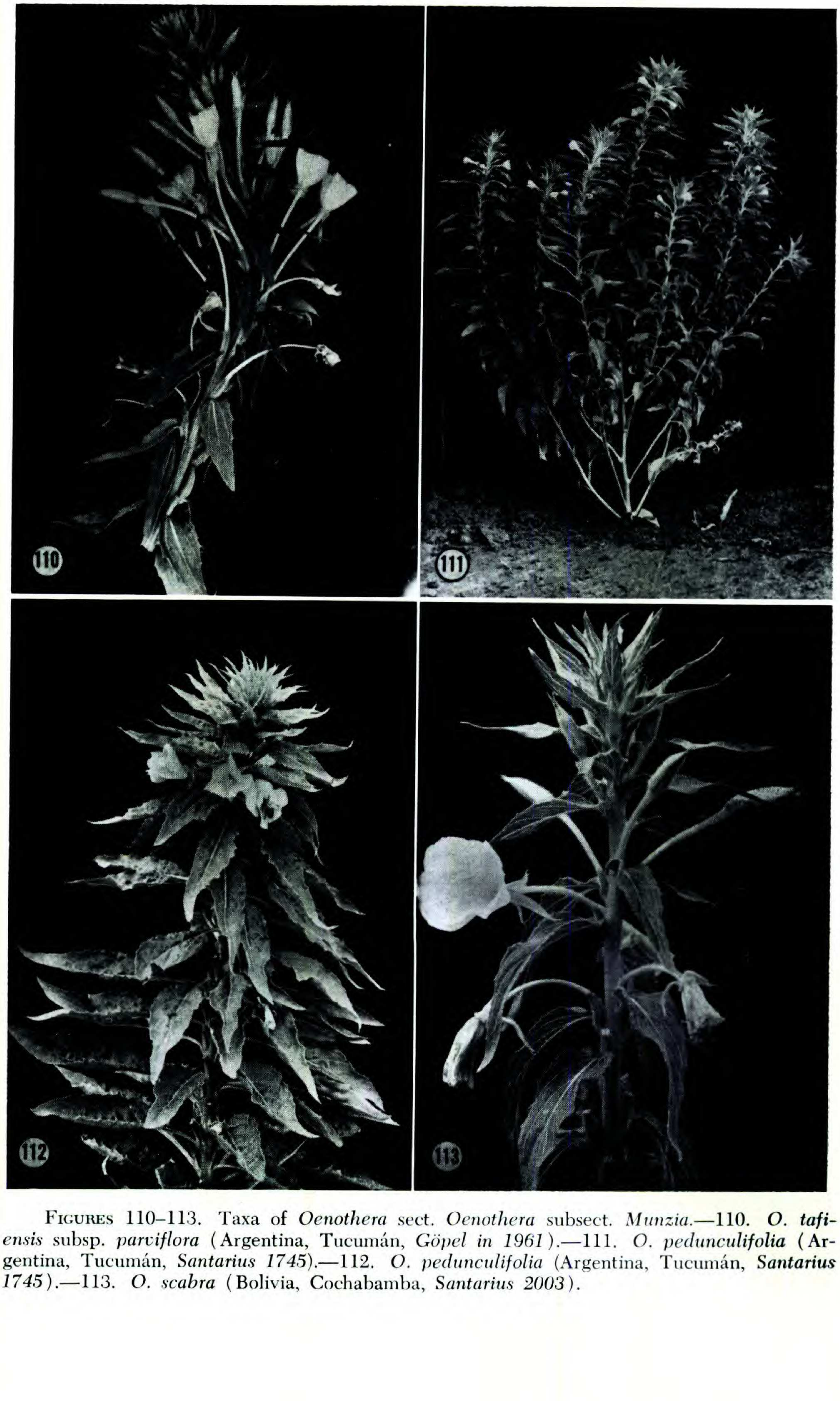
Plantae nunquam e rosula compacta foliosa rames facientes, ad finem caulem principalem simplicem vel 1–3-ramosem producti. Folia rosulae ellipticala, lamina in petiolum ± gradatim decrescens, 6–8 cm longa, 1–1.5 cm lata. Tubus floralis 4–5.5 cm longus. Gemmae ambito oblongae, 1–1.5 cm longae, flavovirides, junctura sepalorum tubo florali rubro-fasciatae; apices sepalorum divergentes. Petala 1.5–2 cm longa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Plant never forming side branches from the compact, leafy rosette, but ultimately elongating and forming a main stem which is either unbranched or has 1–3 side branches. Rosette leaves elliptical, ± abruptly narrowed to the petiole, 6–8 cm long, 1–1.5 cm wide. Floral tube 4–5.5 cm long. Buds oblong in outline, 1–1.5 cm long, yellowish green, red striped at the junction of the sepals with the floral tube; apices of the sepals divergent. Petals 1.5–2 cm long. Anthers 6–7 mm long. Filaments 12–16 mm long. Style 5–7 cm long. Stigma lobes 3–4 mm long. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botnical Garden of Düsseldorf, Germany, 25 July 1972. Source: Argentina, Prov. Tucumán, Villa Nougés near Tucumán, *G. Göpel in 1961** (MO-2155397, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 229): Known only from the type locality.

Specimens examined from cultivated plants: *Göpel in 1961** (DUSS, M, MO).



FIGURES 110–113. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—110. *O.* ***tafiensis*** subsp. *parviflora* (Argentina, Tucumán, *Göpel in 1961*).—111. *O.* ***pedunculifolia*** (Argentina, Tucumán, *Santarius 1745*).—112. *O. pedunculifolia* (Argentina, Tucumán, *Santarius 1745*).—113. *O. scabra* (Bolivia, Cochabamba, *Santarius 2003*).

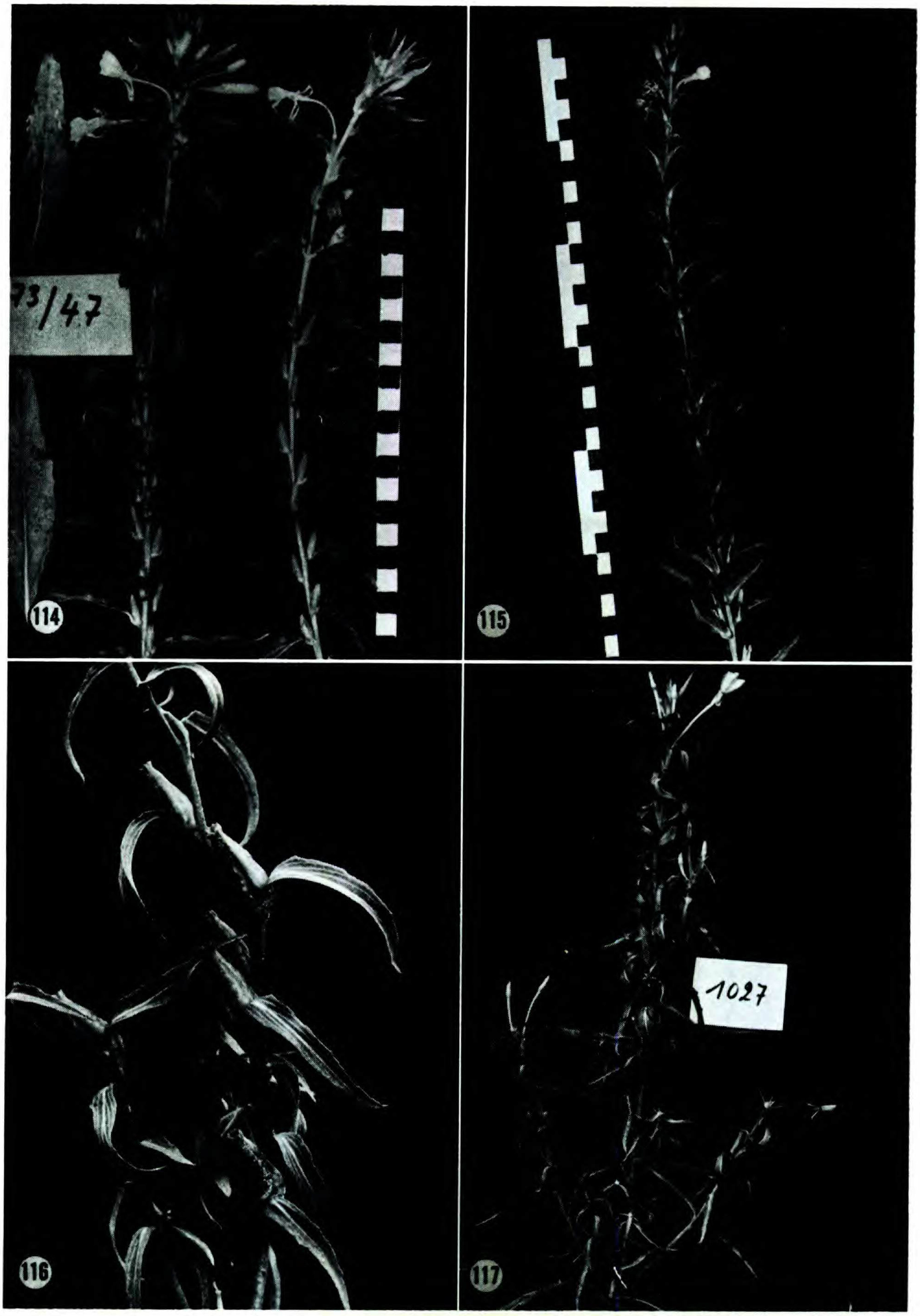
This strain, which I consider so closely related to *O. tafiensis* that the two are best regarded as subspecies of a single species, seems to have contributed its genome to *O. acuticarpa*, a species that has derived its second genome from *O. affinis*. *Oenothera tafiensis* subsp. *parviflora* and *O. acuticarpa* both were collected by Mr. G. Göpel at the same locality. When plants of *O. acuticarpa* are self-pollinated in cultivation, chromosomally homozygous individuals typical of *O. tafiensis* subsp. *parviflora* appear in the progeny, but none representative of the genome derived from series *Allochroa* specifically *O. affinis*. See also the remarks under *O. acuticarpa*.

7. **Oenothera pedunculifolia** Dietrich, sp. nov.—FIGS. 32–34, 111–112, 198.

Herba annua rosulata, 7–12 dm alta, caulis principalis ± ramosus, e rosula ramis nullis. Planta dense solumque strigulosa. Folia rosulae oblanceolata vel anguste obovata, breviter acuta, lamina in petiolum gradatim decrescens, 15–20 cm longa, 3–4(–5) cm lata; folia caulina anguste elliptica vel elliptica, acuta, basi anguste cuneata, petiolata, 6–15 cm longa, 2–4(–5) cm lata; bractea anguste elliptica, acuta, basi anguste cuneata, petiolata, 5–8 cm longa, 1.5–2.5 cm lata; folia laete virides, ± regulariter acuteque serrata. Inflorescentia plerumque simplex, floribus confertissima, quum flores aetatem 4–6 dies attingentes habeant perfecte elongata. Tubus floralis 2.5–5.5 cm longus. Gemmae ambito anguste lanceolatae vel lanceolatae, flavidae, 2–3 cm longae, 5–7 mm crassae; apices sepalorum 2.5–3.5 mm longi, erecti vel divergentes. Petala latissime obovata, retusa, 2–4 cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato. Ovarium 7–9 mm longum. Capsula 1.5–2 cm longa, 4–5 mm crassa. Semina ambito elliptica vel late elliptica, 0.8–1 mm longa, 0.4–0.5 mm lata, plerumque porphyrio punctulata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Erect annual herb, forming a rosette, 7–12 dm tall. Rosette giving rise to a ± branched main stem, but never with basal shoots from the rosette. Entire plant densely and exclusively strigillose. Rosette leaves oblanceolate to narrowly obovate, short-acute, ± abruptly narrowed to the petiole, 15–20 cm long, 3–4(–5) cm wide; cauline leaves narrowly elliptic to elliptic, acute, narrowly cuneate at the base, petiolate, 6–15 cm long, 2–4(–5) cm wide; bracts narrowly elliptic, acute, narrowly cuneate at the base, petiolate, 5–8 cm long, 1.5–2.5 cm wide; leaves bright green, ± plane at the margins and ± regularly and sharply serrate. Inflorescence mostly unbranched, very thick-set with flowers, with 4–6 flowers opening per day. Floral tube 2.5–5.5 cm long. Buds narrowly lanceolate to lanceolate in outline, yellowish, 2–3 cm long, 5–7 mm thick; apices of the sepals erect or spreading, 2.5–3.5 mm long. Petals very broadly obovate, retuse, 2–4 cm long. Anthers 7–10 mm long. Filaments 15–20 mm long. Style long, the stigma held above the anthers at anthesis. Stigma lobes 4–5.5 cm long. Ovary 7–9 mm long, 3.5–6.5 cm long. Capsule 1.5–2 cm long, 4–5 mm thick. Seeds elliptic to broadly elliptic in outline, 0.8–1 mm long, 0.4–0.5 mm thick, usually flecked with dark reddish brown. Self-compatible but modally outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: December–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 24 July 1973. Source: Argentina, Prov. Tucumán, Valle de Tafí, at km 46 of Ruta 307, 15 km before Tafí del Valle, 1,800 m, 12 Mar. 1968, *K. A. Santarius 1745* (MO-2155702, holotype; CTES, DUSS, M, isotypes).



FIGURES 114–117. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—114. *O. scabra* (Peru, Ayacucho, *Santarius 2251*).—115. *O. rubida* (Peru, Arequipa, *Santarius 2101*).—116. *O. tarijensis* (Bolivia, Tarija, *Santarius 1924*).—117. *O. recurva* (Bolivia, Tarija, *Santarius 1955*).

Distribution (Fig. 230): Foothills of the Andes in the provinces of Tucumán and Catamarca, Argentina, 1,500–2,000 m elevation.

Specimens examined from cultivated plants:

ARGENTINA. TUCUMÁN: Valle de Tafí, 1500–1800 m, *Santarius 1745**, *1747**, *1754**, *1760*, *1762**, *1769**, *1781**, *1785*, *1786** (DUSS; *1747*, *1781* also CTES; *1745*, *1747*, *1781* also M; *1745*, *1747*, *1754*, *1769*, *1781*, *1786* also MO).

Additional specimens examined:

ARGENTINA. TUCUMÁN: Valle de Tafí, *Bruch in 1908* (NY); *Diers 320* (SI). Villa Nougés, 1,000 m, *Venturi 2418* (BAB, GH, LIL, POM, SI, US), *204* (POM). Aconquija, Esquina Grande, 1,560 m, *Lillo 1570* (LIL). Malamala, 1,950 m, *N.N. in 1901* (LIL-80370). Cerro de Garabatal near Siambón, *Lorentz & Hieronymus 854* (CORD, GOET). Río Cochuna, 1,700 m, *Schreiter 10481* (F, LIL). Dep. Monteros, Río de los Sosas, km 33 "La Heladera," *Jones 10380* (BAA). Dep. Chicligasta, Las Lagunas near Clavillo, ca. 1,680 m, *Munz 15467* (F, GH, NY, POM, US). CATAMARCA: El Candado, *Jörgensen 1058* pro parte (LIL). El Clavillo near Andalgala, *Jörgensen 1560* pro parte (MO). Río Prisavil, 1,600 m, *Brücher in 1949* (LD, S).

Like *O. tafiensis*, *O. peduncularifolia* is in some respects intermediate between the potentially biennial (species 1–5) and strictly annual (species 8) members of the subsection. In contrast to all other species of the group, *O. pedunculifolia* always has clearly petiolate bracts. In habit and probably also in actual relationship it seems closest to *O. tafiensis*, from which it can be separated by its better developed branching; sharply toothed leaves; bright green hue, in contrast to the gray green of *O. tafiensis*; and shorter capsules.

Hybrids between these two species have been found. The progeny of *Santarius 1781* included an intermediate plant which had a ring of 6 and 4 bivalents in meiosis. Some intermediate plants, on the other hand, are chromosomally homozygous (e.g., *Santarius 1747*), which suggests that populations of the two species exist with undifferentiated chromosomal end arrangements.

8. **Oenothera scabra** Krause, Repert. Spec. Nov. Regni Veg. 1: 168. 1905.—Figs. 9, 28, 113–114, 173, 199–200.

O. campylocalyx sensu Munz & Johnston, Contr. Gray Herb. 75: 22. 1925, pro parte.

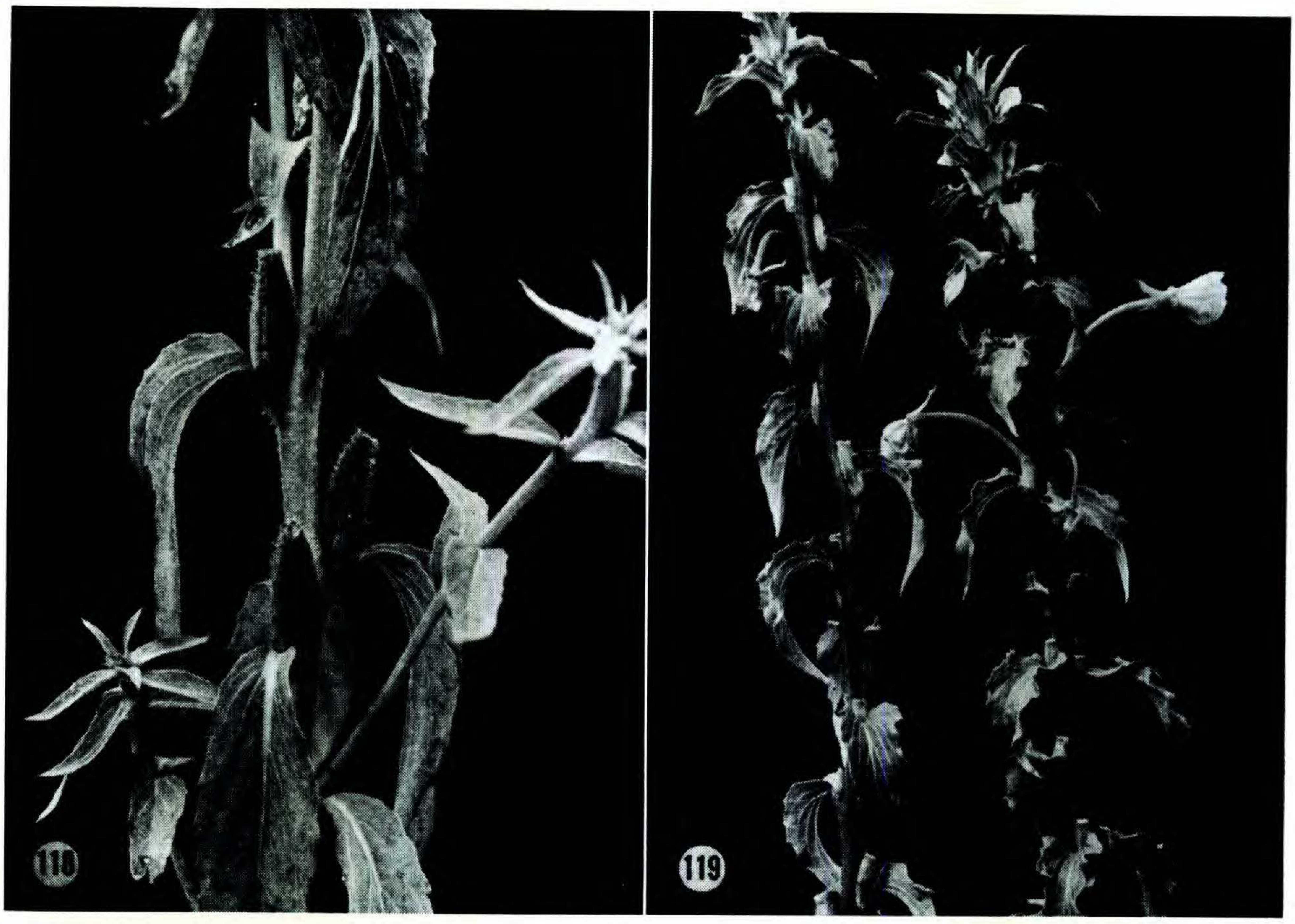
O. campylocalyx sensu Macbride, Field. Mus. Nat. Hist., Bot. Ser. 13(4): 535. 1941, pro parte.

O. burkartiana Bartlett, Darwiniana 6: 208. 1943. TYPE: Argentina, Prov. Salta, Dep. Guachipas, "Pampa Grande," 1,600 m, 27 Apr. 1942, *A. T. Hunziker 1738* (SI, holotype; CORD, LIL, isotypes).

O. curvifolia Fischer, Feddes Repert. Spec. Nov. Regni Veg. 64: 235. 1962. TYPE: Cultivated in the Botanical Garden of Erlangen, *Fischer* (ER).

O. curvifolia "Erlangen" Cleland, Jap. J. Genet. 43: 332. 1968.

Erect annual herb, not forming a rosette, 4–15 dm tall. Main stem unbranched or moderately to extensively branched. Entire plant densely, sparsely, or not strigillose, thickly to sparsely clothed with erect, long-villous pubescence, and often also somewhat glandular-pubescent. Cauline leaves very narrowly elliptic to elliptic or narrowly lanceolate to narrowly ovate, acute, acute to obtuse at the base, sessile or short-petiolate, 5–15 cm long, 1–4 cm wide; bracts narrowly elliptic to oblanceolate, acute, acute to obtuse at the base, sessile or very shortly petiolate, 4–10 cm long, 1–3 cm wide; leaves plane or evidently undulate at the margins, ± regularly or irregularly and sinuately serrate, the teeth blunt. Inflorescence branched or not. Flowers seldom or never overtop-



FIGURES 118–119. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia.*—118. *O. sandiana* (Peru, Cuzco, *Santarius 2307*).—119. *O. sandiana* (Bolivia, La Paz, *Santarius 2018*).

ping the apex of the stem. Floral tube 2.5–5(–7.5) cm long. Buds narrowly oblong to oblong or narrowly lanceolate to lanceolate in outline, 1–3.5 cm long, 4–6 mm thick, yellowish green, often red striped at the junction of the sepals with the floral tube; apices of the sepals erect or spreading, 1–3 cm long. Petals very broadly obovate, usually retuse, yellow, 2.5–3.5 cm long. Anthers 5–11 mm long. Filaments 8–25 mm long. Style long, the stigma elevated above the anthers at anthesis, or short, the anthers shedding pollen directly on the stigma at anthesis, 3.5–8(–9.5) cm long. Stigma lobes 3–6 mm long. Ovary 5–10 mm long. Capsule 1.5–2.5 cm long, 5–7 mm thick. Seeds 0.8–1.3 mm long, 0.4–0.6 mm thick, elliptic to broadly elliptic in outline, brown, often flecked with dark reddish brown. Self-compatible; modally outcrossing or self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents* or ring of 4 and 5 bivalents** at meiotic metaphase I). Flowering time: December–May.

Type: Bolivia, Dep. Tarija, shrubby places along a stream, 2,000 m, 30 Dec. 1903, *K. Fiebrig 2434* (B, destroyed in World War II, UC-292686-7 fragments and photographs, F and POM photographs; G, K, L, LY, isotypes).

Distribution (Fig. 231): Andes from the department of Ayacucho in Peru to the province of La Rioja in Argentina, 1,000–3,200 m elevation.

Specimens examined from cultivated plants:

PERU. AYACUCHO: Ucros, about 116 km behind Ayacucho at road to Andahuaylas, 3,150 m, *Santarius 2251** (CTES, DUSS, M, MO).

BOLIVIA. COCHABAMBA: Incachaca, 2,250 m, *Santarius 2003**, *2007** (DUSS, M, MO; *2003* also CTES).

ARGENTINA. JUJUY: Quebrada de Yala, 1,700 m, *Diers in 1959** (CTES, DUSS, M, MO). CATAMARCA: Dep. Ambato, Ruta 62, 19 km N of Singuil, *Hunziker 9181*** (CTES, DUSS, M, MO).

CULTIVATED: *O. scabra* from Erlangen, received 1960* (CTES, DUSS, M, MO). *O. curvifolia* from Erlangen, received 1962* (CTES, DUSS, M, MO).

Additional specimens examined:

PERU. AYACUCHO: Allate, *Soukup 481* (F). CUZCO: Ollantaytambo, 3,000 m, *Cook & Gilbert 294* (US). PUNO: Carabaya near Antapampa, 4,180 m, *Vargas 7002* pro parte (LIL). MOQUEQUA: Carumas, 3,000 m, *Weberbauer 7283* (BM, F, POM, S, US).

BOLIVIA. LA PAZ: Titicaca, *N.N.* (K). Titicaca, Isla del Sol, 3,840 m, *Buchtien 4661* (US). Larecaja, vicinity of Sorata, 2,690–3,000 m, *Mandon 627* (GH, pro parte, P, W), 3,200 m, *628* (BM, K, LE, P, S, W). COCHABAMBA: Chapare, Incachaca, 2,200 m, *Steinbach 9145* (BM, F, G, GH, K, LIL, MO, NY, S). ORURO: Choro, ca. 2,130 m, *Brooke 6128* (BM). CHUQUISACA: Serrano, *Cárdenas 4114* (US). TARIJA: Tucumilla, 2,800 m, *Fiebrig 3351* (P). Vicinity of Tarija, 1,700 m, *Zelada 40* (LIL).

ARGENTINA. JUJUY: Dep. Capital, Lagunas de Yala, *Cabrera & Fabris 17478* (BAA, LP); *Cabrera et al. 21318* (LP). Yala, 2,086 m, *Romero 34* (LIL). Termas de Reyes, *Romero in 1947* (LIL). Almiron Luzano, *N.N. 88* (LIL-347275). Tumbaya, Volcán Chilcayo, 2,300 m, *Fabris 6089* (BAA). Santa Barbara, Los Monteros, *Cabrera 5205* (LP). Valle Grande, 2,600 m, *Burkart 115959* (SI). Río Chico, 1,258 m, *Schreiter 2834* (LIL). SALTA: La Ollada, *Lahitte 49842* (BAB). Orán, San Andres, 1,800 m, *Pierotti 294* (LE, LIL, NY, UC), *1378* (LIL, NY, UC). Río Cañas near Orán, *Willirich 351* (LIL). Valle de Lerma, *Tabala 17* (LIL). Campo Quijano, Río Toro, *Krapovickas 10051* (LIL). TUCUMÁN: Tafí, *Lillo 4155* (LIL, MO). Las Peñas Azules, 3,200 m, *Olea in 1933* (S). San Javier, *Rocha 1001* (LIL). Río Chico, Escaba, 2,250 m, *Monetti 1841* (GH), *14900* (LIL). Burroyacú, Duraznillo, 1,000 m, *Monetti 2051* (GH). CATAMARCA: Andalgala, *Jörgensen 1560* pro parte (GH). Between Andalgala and Capillitas, *O'Donell & Meyer 5215* (LIL). Huillapima, *Spegazzini 28673* (BAB). Sierra de Ambato, Casa de Cubas to Las Lajas, 3,300 m, *Hunziker et al. 20086* (CORD). Pomán, Las Ciénagas, 2,000 m, *Vervoorst 3503* (LIL). Pomán, Sierra de Ambato, Cerro Manchado, 2,500–2,750 m, *Hunziker 20465* (CORD, MO). LA RIOJA: Sierra de Famatima, Chilecito, Mina El Oro, 3,000 m, *Calderon 1079* (BAA).

Oenothera scabra never forms a rosette, but grows soon after germination from only a few basal leaves to an erect, often well-branched, plant. Another characteristic is the erect villous pubescence.

Even though there is a considerable amount of natural variation, it is not possible to delimit taxonomically useful races within *O. scabra*. There are plants of *O. scabra* (e.g., *Cárdenas 4114*, *Hunziker 9181*) that totally lack the strigillose pubescence otherwise found in all species of series *Renneria*. They are therefore exclusively villous and glandular-pubescent, a characteristic that otherwise occurs only in the species of series *Allochroa* and *Clelandia*. Since, in addition the capsule may often be broadly cylindrical, one is led to the conclusion that *O. scabra* may be closely related not only to *O. affinis*, which has large flowers and a long floral tube, but also to the small-flowered *O. indecora*. Both are exclusively villous and glandular-pubescent.

9. **Oenothera rubida** Rusby, Bull. New York Bot. Gard. 8: 110. 1912.—FIG. 115.

O. laciniata sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 537. 1941, pro parte.

Erect annual herb, not forming a rosette, 5–10 dm tall. Plants branched from the base upward. Entire plants densely strigillose, and also erect long-villous in the region of the inflorescence. Cauline leaves very narrowly elliptic to narrowly elliptic, acute, narrowly cuneate at the base, short-petiolate, 2.5–7 cm

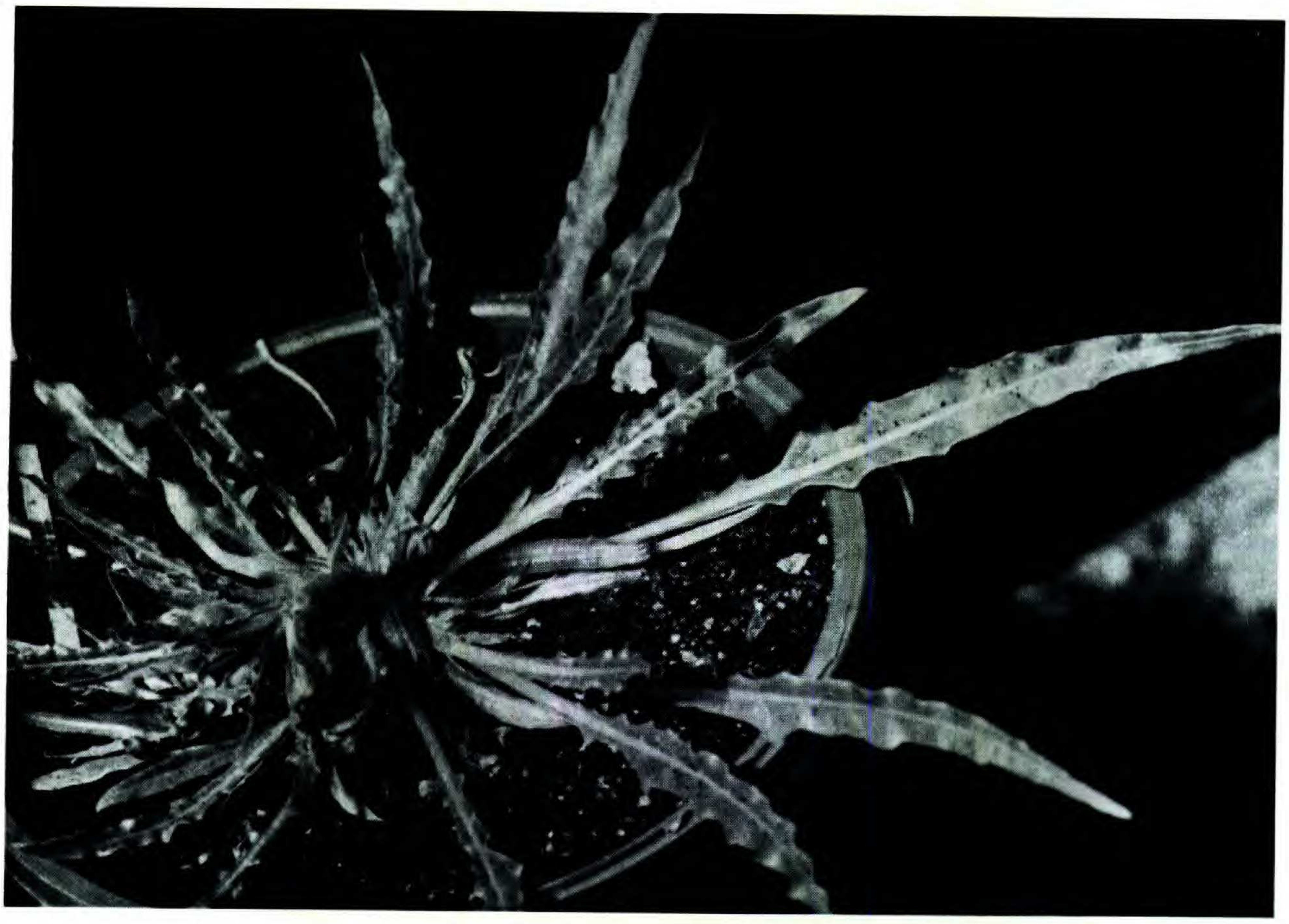


FIGURE 120. *Oenothera nana* (Argentina, Jujuy, *Santarius 1895*); *Oenothera* sect. *Oenothera* subsect. *Munzia*.

long, 0.5–1.5 cm wide; bracts narrowly elliptic to lanceolate, acute, acute to truncate at the base, sessile or very short-petiolate, 3–7 cm long, 1–2 cm wide; leaves usually undulate at the margins and ± regularly and sharply serrate. Inflorescence simple or branched. Floral tube 1–2 cm long. Buds oblong to narrowly ovate in outline, ca. 1 cm long, 4–5 mm thick; apices of the sepals erect or divergent, 2–3 mm long. Petals very broadly obovate, 0.8–1.2 cm long. Anthers 4–6 mm long. Filaments 6–8 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.5–2.8 cm long. Stigma lobes 3–5 mm long. Ovary 8–10 mm long. Capsule 1.8–2.5 cm long, 4–5 mm thick. Seeds 1–1.5 mm long, 0.7–0.8 mm thick, ± obtusely angular, dark brown to black. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–May.

Type: Peru, Dep. Arequipa, Arequipa, 2,460 m, *R. S. Williams 2524* (NY).

Distribution (Fig. 226): Mountain slopes in the department of Arequipa, Peru, and the province of Tarapacá, Chile, 2,200–3,500 m elevation.

Specimens examined from cultivated plants:

PERU. AREQUIPA: Near Arequipa, road Chihuata/Puno, 2,700 m, *Santarius 2094, 2100*, 2101, 2114, 2119** (DUSS; *2100, 2119* also CTES, M; *2094, 2100* also MO).

Additional specimens examined:

PERU. AREQUIPA: Río Chile near Aequipa, ca. 2,530 m, *Munz 15538* (NY, POM, US). Quebrada de Lazaro, ca. 2,800 m, *Munz 15529* (NY, POM, US). Chachani mountains, *Hinck-*

ley 68 (GH, US). Morro Verde, 18 km above Yura, 2,870–3,000 m, *Straw 2351* (US, USM). Arequipa, 3,100–3,300 m, *Pennell 14279* (F). Characato, 2,600 m, *Vargas in 1949* (RSA). Chuquibamba near Condesuyos, ca. 3,200 m, *Stafford 1178* (K). Río Chile near Tingo, ca. 2,290 m, *Munz 15504* (F, G, GH, NY, POM, US). Arequipa, 2,300 m, *Günther & Buchtien 630* (HBG). Cachendo, 650 m, *Günther & Buchtien 2034* (HBG).

CHILE. TARAPACÁ: Pampa Ossa from Arica to La Paz, 2,200 m, *Ricardi 3438* (CONC). Pachica, *Ortega in 1880* (SGO). Libaya, *Rahmer in 1885* (SGO). Tarapacá, *Philippi* (CORD).

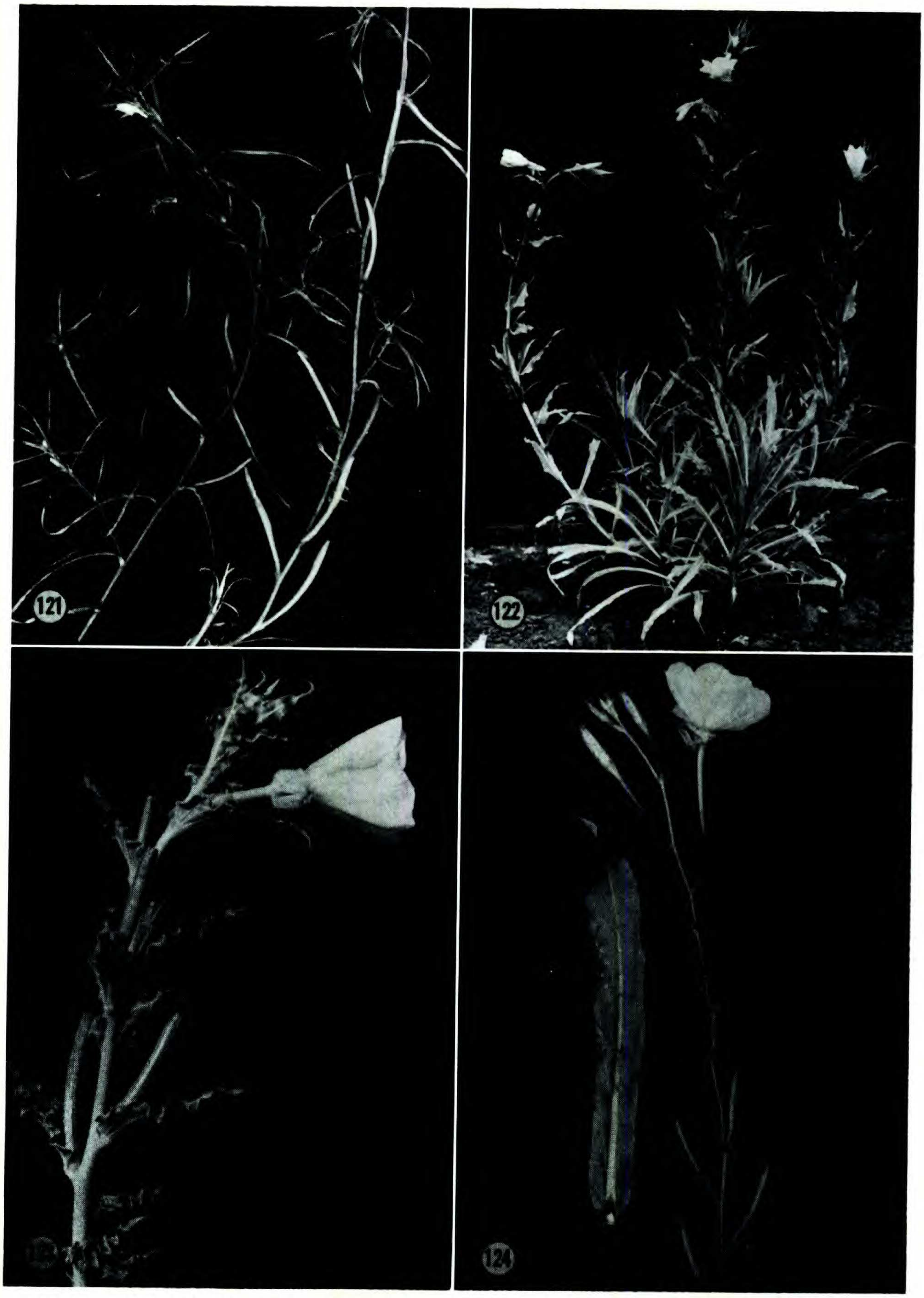
Oenothera rubida occurs with *O. peruana* and *O. verrucosa.* Although both of its chromosomal complexes are evidently derived from *O. peruana,* it is so clearly distinguished from that species by its more lax inflorescence, shorter capsules, and smaller flowers that it seems best to treat it as distinct. In addition, both genomes of the complex heterozygote *O. rubida* seem to include segments of the genomes of *O. scabra* and *O. verrucosa,* and so are not "pure" *peruana.* The inflorescence, which is often erect-villous, and the lack of a rosette, both seem to be indications of the influence of *O. scabra,* whereas the relatively slender capsule may be a result of the influence of *O. verrucosa.* Whether these influences represented hybridization between the species involved, or indicate that *O. rubida* originated before the full differentiation of the three other species under discussion from one another, is uncertain. One might assume, however, from the very limited range of *O. rubida* that it is a species of recent derivation, since there is no obvious reason why it could not spread as easily as the much more widely distributed *O. sandiana.* On the other hand, the complex heterozygosity of *O. rubida* seems to indicate that it is well established and that its persistence in nature is assured since hybrids with other entities have not been observed and are at the most very infrequent. This would tend to indicate a relatively great age, and the question must be left unsettled for the present.

10. **Oenothera tarijensis** Dietrich, sp. nov.—FIGS. 26, 116.

O. campylocalyx sensu Munz & Johnston, Contr. Gray Herb. 75: 22. 1925, pro parte.

Herba annua, non rosulata, ubique ramosa, 4–7 dm alta. Planta tota dense strigulosa, circum inflorescentiam pilis longis adpressis praedita. Folia caulina linearia vel angustissime elliptica, acuta, lamina in petiolum brevem gradatim decrescens, 7–20 cm longa, 1–1.5 cm lata; bractea anguste lanceolata, acuta, basi acuta vel rotundata, 4–7 cm longa, 0.5–1 cm lata; bractea sub anthesi maturitateque plerumque ad angulum 90° patentes; folia irregulariter obtuseque serrata. Inflorescentia simplex vel ramosa. Tubus floralis 3–5.5 cm longus. Gemmae ambito lanceolatae, 1–1.5 cm longae, 4–5 mm crassae, junctura sepalorum tubo florali anguste rubro-fasciatae; apices sepalorum divergentes, ca. 2 mm longi. Petala latissime obovata, lutea, saepe rubro basi et secus venos suffusa, 1.5–2 cm lata. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 9–13 mm longum. Capsula 2.5–3 cm longa, 5–7 mm crassa. Semina obtuse angulata, 1.3–1.5 mm longa, 0.9–1.1 mm lata, brunnea vel subnigra. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, branched throughout, 4–7 dm tall. Entire plant densely strigillose, with an admixture of appressed long-villous pubescence in the region of the inflorescence. Cauline leaves linear to very narrowly elliptic, acute, narrowed to a short petiole, 7–20 cm long, 1–1.5 cm wide; bracts narrowly lanceolate, acute, acute to rounded at the base, 4–7 cm long, 0.5–1 cm wide; bracts in flower and fruit mostly spreading at right angles; leaves usually plane at the margins and irregularly and bluntly serrate.



FIGURES 121–124. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—121. *O. mendocinensis* (Argentina, Chubut, *Santarius 1354*).—122. *O. odorata* (Argentina, Río Negro, *Santarius 680*).—123. *O. odorata* (Argentina, Buenos Aires, *Santarius 329*).—124. *O. ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul, *Hackbart in 1966*).

Inflorescence simple or branched. Floral tube 3–5.5 cm long. Buds lanceolate in outline, red striped at the junction of the sepals with the floral tube, 1–1.5 cm long, 4–5 mm thick; apices of the sepals divergent, ca. 2 mm long. Petals very broadly obovate, yellow, often suffused with red at the base and along the veins, 1.5–2 cm long. Anthers 5–8 mm long. Filaments 10–14 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 4–6.5 cm long. Stigma lobes 3.5–6.5 mm long. Ovary 9–13 mm long. Capsule 2.5–3 cm long, 5–7 mm thick. Seeds 1.3–1.5 mm long, 0.9–1.1 mm thick, obtusely angular, dark brown to almost black. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: January–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 25 July 1972. Source: Bolivia, Dep. Tarija, between km 38 and 36 at the road from Villazón to Tarija, 3,200–3,300 m, 19 Mar. 1968, K. A. *Santarius 1924* (MO-2155393, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 227): Andes of Bolivia, 2,500–3,700 m elevation.

Specimens examined from cultivated plants:

BOLIVIA. TARIJA: At road from Villazón to Tarija, 38–30 km before Tarija, 2,900–3,300 m, *Santarius 1924**, *1949*, *1950**, *1955** (DUSS; 1955 also CTES; *1924*, *1955* also M; *1924*, *1949*, *1955* also MO).

Additional specimens examined:

BOLIVIA. LA PAZ: Vicinity of Sorata, 2,650–3,000 m, *Mandon 627* pro parte (W). Obrajes, 3,600 m, *Parodi 10152* (BAA, MO). La Paz, 3,550 m, *Buchtien 39* pro parte (US). TARIJA: Piños near Tarija, *Fiebrig 3358* (BM, GH, GOET, K, L, M, P, S). La Aguada near Villazón, *Balls 6120* (K, UC, US).

Oenothera tarijensis has one complex each from *O. versicolor* and *O. longituba*; the former (*Santarius 1946*) occurred with *O. tarijensis* at its type locality. The small leaves and flower color of *O. tarijensis* seem to be derived from *O. versicolor*, whereas the intermediate length of its floral tube can be attributed to *O. longituba*. Very likely the influence of *O. scabra* is also important in *O. tarijensis*, possibly through hybridization and partitioning of the genome, judging from the annual habit and lack of a rosette in both species, in contrast to the situation in *O. versicolor* and *O. longituba*.

11. **Oenothera recurva** Dietrich, sp. nov.—FIGS. 27, 117.

Herba annua erecta, non rosulata, omnino ramosa, 5–10 dm alta. Plantae dense strigulosae, ad basin glabescentes, circum inflorescentiam pilis longis erectis vel adpressis praeditae. Folia caulina anguste elliptica vel lanceolata ad anguste ovata, acuta, basi acuta vel truncata, sessilia vel breviter petiolata, 7–18 cm longa, (1–)1.5–2.5 cm lata; bractea lanceolata vel ovata, acuta, basi truncata, sessilia, 3–6 cm longa, 1–2 cm lata; bractea sub anthesi maturitateque plerumque sursum arcuata; folia irregulariter obtuseque serrata. Inflorescentia simplex vel ramosa, pro ratione laxa ut in *O. tarijense*, flore uno solo in diem aperiente. Tubus floralis (5–)6–9 cm longus. Gemmae ambito lanceolatae, saepe junctura sepalorum tubo florali rubrofasciatae, 1.5–2 cm longae, 5–6 mm crassae; apices sepalorum erecti, ca. 2 mm longi. Petala latissime obovata, lutea, raro rubro basi et secus venos suffusa, 2–3 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium ca. 10 mm longum. Capsula (1.5–)2–3 cm longa, 5–6 mm crassa. Semina 1.2–1.6 mm longa, 0.6–0.8 mm crassa, ± obtuse angulata, brunnea. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

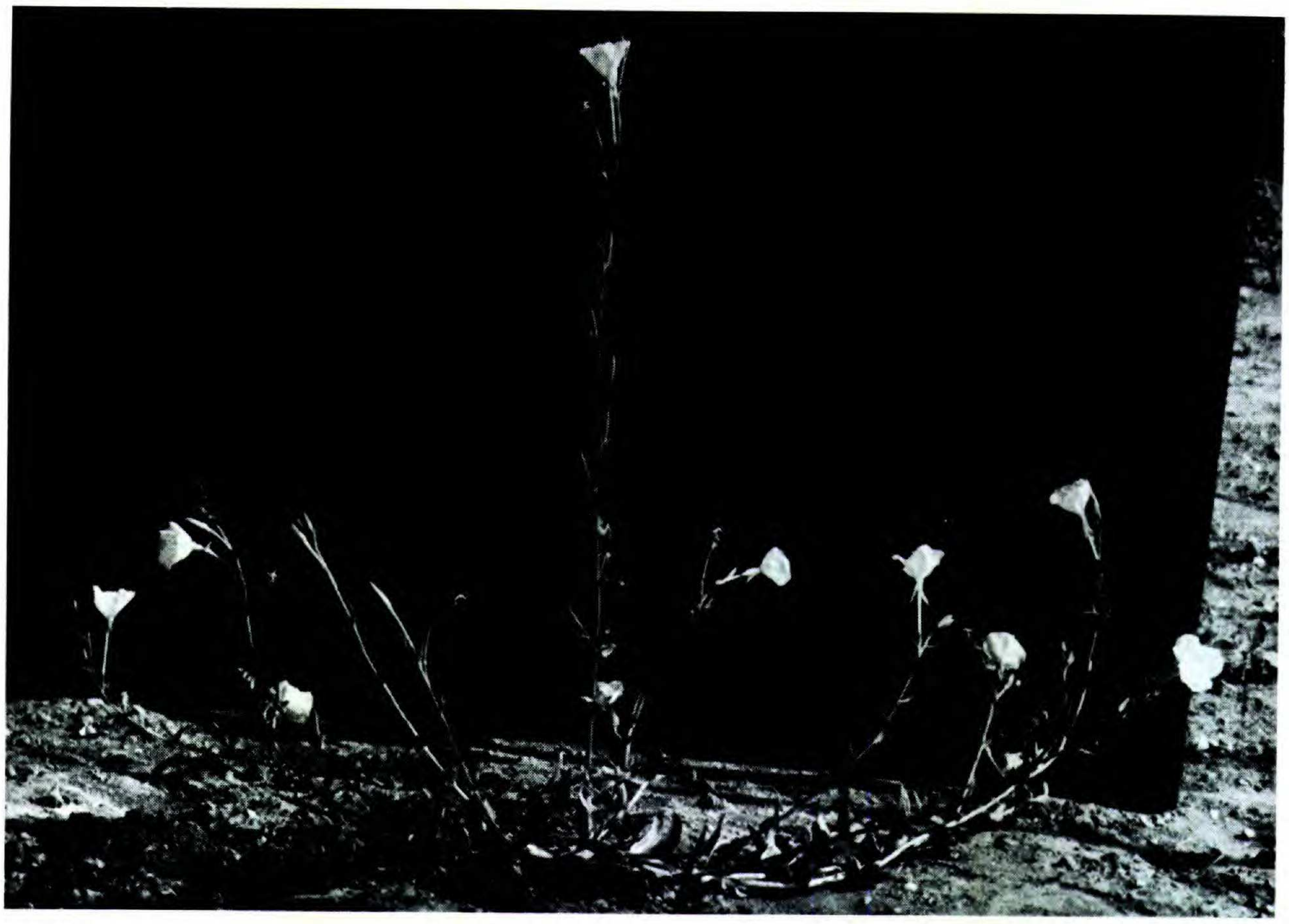


FIGURE 125. *Oenothera ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul, *Hackbart in 1966*); *Oenothera* sect. *Oenothera* subsect. *Munzia*.

Erect annual herb, not forming a rosette, branched throughout, 5–10 dm tall. Plants densely strigillose, glabrescent near the base, with an admixture of erect or appressed long-villous pubescence in the region of the inflorescence. Cauline leaves narrowly elliptic or lanceolate to narrowly ovate, acute, acute to truncate at the base, sessile or short-petiolate, 7–18 cm long, (1–)1.5–2.5 cm wide; bracts lanceolate to ovate, acute, truncate at the base, sessile, 3–6 cm long, 1–2 cm wide; bracts in flower and fruit mostly curving upward; leaves undulate at the margins and irregularly and bluntly serrate. Inflorescence simple or branched, relatively lax as in *O. tarijensis*, with only a single flower opening each day. Floral tube (5–)6–9 cm long. Buds lanceolate in outline, often red striped at the junction of the sepals with the floral tube, 1.5–2 cm long, 5–6 mm thick; apices of the sepals erect, ca. 2 mm long. Petals very broadly obovate, yellow, rarely suffused with red at the base and along the veins, 2–3 cm long. Anthers 6–8 mm long. Filaments 10–17 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, (6–)7–10 cm long. Stigma lobes 5–7 mm long. Ovary ca. 10 mm long. Capsule (1.5–)2–3 cm long, 5–6 mm thick. Seeds 1.2–1.6 mm long, 0.6–0.8 mm thick, ± obtusely angled, dark brown. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: January–May.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 24 Sep. 1970. Source: Bolivia, Dep. Tarija, between km 32 and

30 at road from Villazón to Tarija, 2,900–3,000 m, 19 Mar. 1968, *K. A. Santarius 1952* (MO-2155699, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 228): Andes of Bolivia from La Paz to Tarija, 2,000–3,600 m elevation.

Specimens examined from cultivated plants:

BOLIVIA. TARIJA: At road from Villazón to Tarija, at km 35 and 32–30, 2,900–3,150 m, *Santarius 1941**, *1952** (DUSS, M, MO; *1941* also CTES).

Additional specimens examined:

BOLIVIA. LA PAZ: La Paz, 3,550 m, *Buchtien 39* pro parte (L, US). Obrajes, 3,550 m, *Buchtien 77* pro parte (K, L). COCHABAMBA: Colomí, Prov. Chaparé, 3,300 m, *Cárdenas 4257* (US). CHAPARÉ: Cerro de Chimoré, 2,300 m, *Troll 1179* (B).

Oenothera recurva has the *longituba*-complex in common with the very similar *O. tarijensis*. It can be distinguished from *O. tarijensis* principally by its broader leaves, longer floral tube, and erect villous pubescence in the inflorescence. Its second chromosomal complex is derived from *O. scabra*, which has very similar pubescence.

Since the chromosomally homozygous *O. versicolor* and *O. scabra* and the complex heterozygotes *O. tarijensis* and *O. recurva* often grow together, it is not surprising that hybrids should occasionally be formed. The progeny of *Santarius 1952* included a plant with a ring of 10 and a ring of 4 chromosomes, and it can only be interpreted as a spontaneous hybrid. As was emphasized in the introduction to this paper, such frequent hybridization suggests that the complex is in an active state of evolution at the present time.

12. **Oenothera sandiana** Hasskarl, Flora 33: 516. 1856; Retzia, Hort. Bogor. Descr. sive Retzia 1: 291. 1858.—FIGS. 118–119, 201–202.

O. weberbaueri Krause, Repert. Spec. Nov. Regni Veg. 1: 168. 1905. TYPE: Peru, Prov. Chicla, stony places along the railroad from Lima to Oroya, 3,720 m, 30 Dec. 1901, *A. Weberbauer 237* (B, destroyed in World War II; UC fragments and photograph, GH and POM photographs).

O. campylocalyx sensu Munz & Johnston, Contr. Gray Herb. 75: 22. 1925, pro parte.

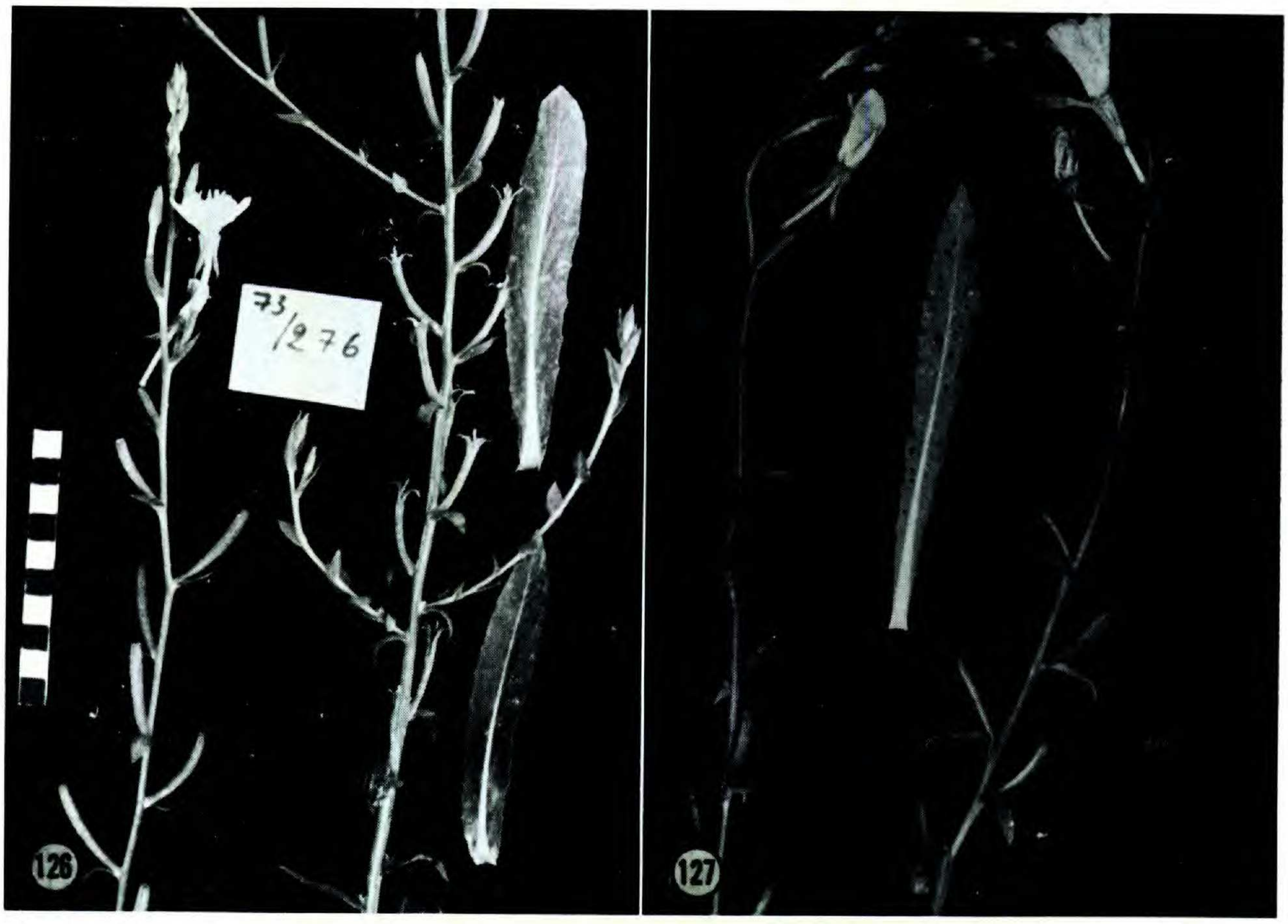
O. campylocalyx sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 535. 1941, pro parte.

O. rubida sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 540. 1941, pro parte.

O. campylocalyx "Erlangen" Haustein, Z. Indukt. Abstammungs-Vererbungsl. 84: 418. 1952; Fischer, Feddes Repert. Spec. Nov. Regni Veg. 64: 237. 1962; Cleland, Jap. J. Genet. 43: 332. 1968.

O. campylocalyx sensu Munz, Opera Bot., Ser. B, 3: 39. 1974, pro parte.

Erect annual herb, not forming a rosette, unbranched or much branched in the lower portions, 3–10 dm tall. Plants densely to sparsely strigillose and also densely to sparsely covered with appressed or erect long-villous pubescence, always more heavily pubescent in the region of the inflorescence. Cauline leaves narrowly elliptic to lanceolate, acute, narrowly cuneate to truncate at the base, sessile or short-petiolate, 5–10 cm long, 1–3 cm wide; bracts lanceolate to narrowly ovate, acute, rounded to truncate at the base, sessile, 3–6(–8) cm long, 1–2.5 cm wide; all leaves plane to evidently undulate at the margins and regularly or irregularly but mostly bluntly serrate; bracts sometimes sinuate, with acute teeth. Inflorescence mostly unbranched, thicker than in *O. tarijensis* and *O. recurva*. Each day 1–3 new flowers opening; flowers sometimes exceeding



FIGURES 126–127. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—126. *O. ravenii* subsp. *argentinae* (Argentina, Buenos Aires, *Santarius 342*).—127. *O. ravenii* subsp. *chilensis* (Chile, Cautín, *Stubbe in 1960*).

the apex of the stem by up to 2 cm. Floral tube 2–5.5 cm long. Buds oblong to narrowly ovate in outline, 1–2 cm long, 3–6 mm thick, usually red striped at the junction of the sepals with the floral tube; apices of the sepals erect or spreading, 1–2 mm long. Petals very broadly obovate, yellow, sometimes reddish at the base and along the veins, 1.5–2.5 cm long. Anthers 3.5–8 mm long. Filaments 7–10 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.5–6.5 cm long. Stigma lobes 3–6 mm long. Ovary 8–10 mm long. Capsule 1.5–2.5 cm long, 4–7 mm thick. Seeds elliptic to broadly elliptic in outline, brown to almost black, very rarely flecked with reddish brown. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14*, ring of 10 and 2 bivalents**, ring of 10 and ring of 4*** or ring of 12 and 1 bivalent**** at meiotic metaphase I). Flowering time: Ecuador and Peru, November–June; Bolivia, December–April.

Type: Cultivated at the Botanical Garden, Bogor, Java, Indonesia, 1855, *J. K. Hasskarl* (presumably at BO, not seen). Source: Peru, Dep. Puno, Sandia, east of Lake Titicaca, 1,500 m.

Distribution (Fig. 229): In the Andes from the department of Lambayeque, Peru to the department of Cochabamba, Bolivia, 2,000–4,000 m elevation, rarely lower. The stations in the provinces of Pinchincha, Latacunga, and Tunguragua in Ecuador, as well as in the province of Tarapacá, Chile, may represent introductions.

Specimens examined from cultivated plants:

Ecuador. PICHINCHA: San Rafael, 3 km S of Quito, *Göpel in 1962** (DUSS, M, MO).

Peru. JUNÍN: Stony slopes at Río Mantaro, on both sides of the railway between km 296 and 298, 3 km SW of Jauja, 3,400 m, *Santarius 2125*, 2126*, 2127*, 2130, 2133, 2135, 2139, 2140*, 2142, 2144, 2152*, 2155, 2158** (DUSS; *2127, 2140, 2152, 2158* also CTES; *2126, 2127, 2140, 2152, 2158* also M; *2126, 2127, 2140, 2142, 2152, 2158* also MO). AYACUCHO: Slopes, W edge of Ayacucho, 2,900 m, *Santarius 2206*, 2210, 2212*, 2215, 2218, 2220, 2224, 2225, 2230, 2231, 2233, 2234* (DUSS; *2212* also CTES, M, SP; *2206, 2212, 2225, 2234* also MO). Ucros, 116 km from Ayacucho on road to Andahuaylas, 3,150 m, *Santarius 2240*, 2241–2249, 2250*, 2252–2255, 2256*, 2257–2259, 2260** (DUSS; *2240, 2256, 2260* also CTES; *2240, 2250, 2256* also M; *2240, 2242, 2248, 2249, 2250, 2256, 2260* also MO; *2250* also CTES, SP). CUZCO: Machu Picchu, 2,700 m, *Santarius 2266*, 2267, 2268, 2269*, 2270, 2271* (DUSS; *2266* also MO); *Göpel in 1962** (DUSS, M, MO). Urubamba valley, along railway between Ollanta and Pachar at km 64.3, 2,750 m, *Santarius 2273***, 2274–2281, 2283–2287, 2289, 2298–2295* (DUSS; *2273, 2285* also MO). Urubamba valley, between Ollantaitambo and Pachar, at km 61.8, 2,800 m, *Santarius 2297***, 2298–2301, 2304–2306* (DUSS; *2297* also CTES, M; *2297, 2300* also MO). Urubamba valley, slopes S of Pisac, 3,050 m, *Santarius 2307*, 2308*, 2309*, 2310–2324* (DUSS; *2309* also CTES; *2308, 2309* also M; *2307, 2308, 2309, 2314, 2317* also MO).

Bolivia. LA PAZ: Slope on east side of Valle de Irpaví, 0.5–1 km N of Calacoto, 3,450 m, *Santarius 2018*, 2021, 2022*, 2023–2025* (DUSS; *2018* also CTES, M; *2018, 2022, 2023* also MO). COCHABAMBA: Ca. 26 km E of Cochabamba on road to Todos Santos, 2,900 m, *Santarius 1974*, 1976**, 1982****, 1986* (DUSS; *1976* also CTES, M; *1976, 1982* also MO), 32 km E of Cochabamba, 3,200 m, *Santarius 1992*, 1993, 1994* (DUSS; *1992* also M, MO).

Cultivated: *O. campylocalyx* from the Botanical Garden in Erlangen, Germany, received 1960* (CTES, DUSS, M, MO).

Additional specimens examined:

Ecuador. TUNGURAGUA: Between Pishilata and Ambato, 2,400–2,700 m, *Solis 9226* (F). COTOPAXI: Saquisili, 2,750 m, *Heiser 6067* (MO). LEÓN: Latacunga, 2,800 m, *Asplund 6929* (G, K, LD, S, US).

Peru. LAMBAYEQUE: Yanahuanca, ca. 3,050 m, *Macbride & Featherstone 1250* (F, GH, US). CAJAMARCA: La Herilla near Contumaza, *Sagasteguí et al. 6429* (US). LA LIBERTAD: Santiago de Chuco, Cachicadán, 3,050 m, *Lopez 449* (USM). Slopes above Yamobamba, ca. 70 km E of Trujillo, 3,000–3,100 m, *Conrad 2717, 2755, 2756, 2757, 2758, 2760, 2763* (MO). ANCASH: Baños de Chancos near Huaraz, ca. 2,750 m, *Sandeman 4618* (K). Ancash, *Raimondi* (USM). LIMA: Río Blanco, Prov. Huarochirí, 3,000–3,500 m, *Killip & Smith 21759* (NY, POM, US); *Macbride & Featherstone 721* (F, GH, US). Infiernillo near Huarochirí, 3,200 m, *Goodspeed et al. 11546* (GH, K, UC). Infiernillo, between San Mateo and Río Blanco, 3,300 m, *Ferreyra 8335* (BM, USM). Surco, 3,000–3,200 m, *Ferreyra 0666* (USM). Atsmita near Tupe, 3,100 m, *Cerrate 1059* (USM). JUNÍN: Prov. Tarma, Chuquishiunca near Huacapistama, between Tarma and San Ramón, 2,000–2,300 m, *Ferreyra 0437* (USM). Yanamayo between Palca and Acobamba, 2,600–2,700 m, *Ferreyra 3768* (US, USM). Hacienda San Juan near Jauja, 3,300 m, *Ferreyra 12918* (USM). Jauja, *Ridoutt 10783* (USM). Huancayo, 3,317 m, *Soukup 3574* (CORD, LIL, MO), *3163* (F); *Chávez 11932, 12430* (USM); *Hoffmann 173* (M). PASCO: Between Salcachupán and Cerro de Pasco, 3,500–3,600 m, *Ferreyra 6601* (USM). HUANCAVELICA: Crocco near Conaica, 3,500–3,550 m, *Tovar 119* (US). Motca, 44 km SE Conaica, 3,400–3,450 m, *Tovar 260* (US). AYACUCHO: Aucará, *N.N. in 1967* (RSA). Apurimac, Abancay, 2,800–3,200 m, *Vargas 8994* (US). Andahuaylas, Chucheros, 3,000–3,200 m, *Riccio 243* (RSA). CUZCO: Urcos, 3,050–3,650 m, *Stafford in 1932* (K). Cerro Sacsahuamán, 3,400 m, *Ferreyra 2678* (USM). Chuspicanchis near Huarcapata, 3,100 m, *Vargas 1785* (GH). Ollantaytambo, *Munz 15543* (POM). 2,900 m, *Herrera 689* (F, US). Urubamba valley, between Yuncapate and Sta. Rita, 2,800 m, *Vargas 2697* (MO). Hacienda Sta. Rita, *Dreyfus 12789* (USM). Puente Urubamba, 2,810 m, *Vargas 7886* (LIL). Paucartambo valley, 3,000 m, *Vargas 671* (MO); 3,300 m, *Woytkowski 228* (USM); *Herrera 3359* (F, POM). Road to Pillahuata, km 79, 2,900 m, *Ugent & Vargas 4415* (K); 2,800 m, *Woytkowski 68* (USM). Hacienda Phuycella, 3,400 m, *Herrera 2979* (US). Alcumbrera near Chateca, 3,450 m, *Herrera 1090* (BM, F, GH, K, MO, US). Machu Picchu, 2,400 m, *Herrera 1989* (F); 2,600 m, *Munz 15546* (POM); ca. 2,130 m, *Sandeman 3,640* (K); *Tutin 1293* (BM). Vicinity of Cuzco, 3,500 m, *Herrera 3* (LIL); 3,000-3,600 m, *Herrera in 1923* (GH, US); *Herrera 3051* (US); *Rose 19065* (US); 3,660 m, *Munz 15541* (NY, POM, US). Pisac near Calca, 3,000 m, *Marin*

25 (F, LIL); *Juzepczuk 10780* (LE). Vitcabamba near Calca, 2,100–2,700 m, *Vargas 3822* (MO). Haciendo Orco near Calca, *Hammarland 588* (S). PUNO: Prov. Carabaya, road between Ollachea and Farina, *Raimondi in 1864* (USM). Ollachea, 2,500 m, *Vargas 6940* (POM). Isla de la Laguna de Titicaca, *Raimondi in 1864* (USM). Road from Puno to Juliaca, 3,800 m, *Ugent 5246* (K). Quicacha, *Raimondi 187* (USM).

BOLIVIA. LA PAZ: Prov. Nor Yungas, Chirca, 2,500 m, *Eyerdam 25352* (F, GH, K, MO, US). La Paz, 3,600 m, *Parodi 10152* (POM); 3,500 m, *Shepard 217* (GH, POM, UC, US); COCHABAMBA: Chaparé, road to Chimoré, 32 km NE Cochabamba, 1,200 m, *Eyerdam 24996* (F, K, UC). Ansalso, between Cochabamba and Vilavila, 2,600 m, *Eyerdam 25078* (F, GH, K, UC).

CHILE. TARAPACÁ: Mamiña, 2,700 m, *Ricardi 4700-1085* (CONC).

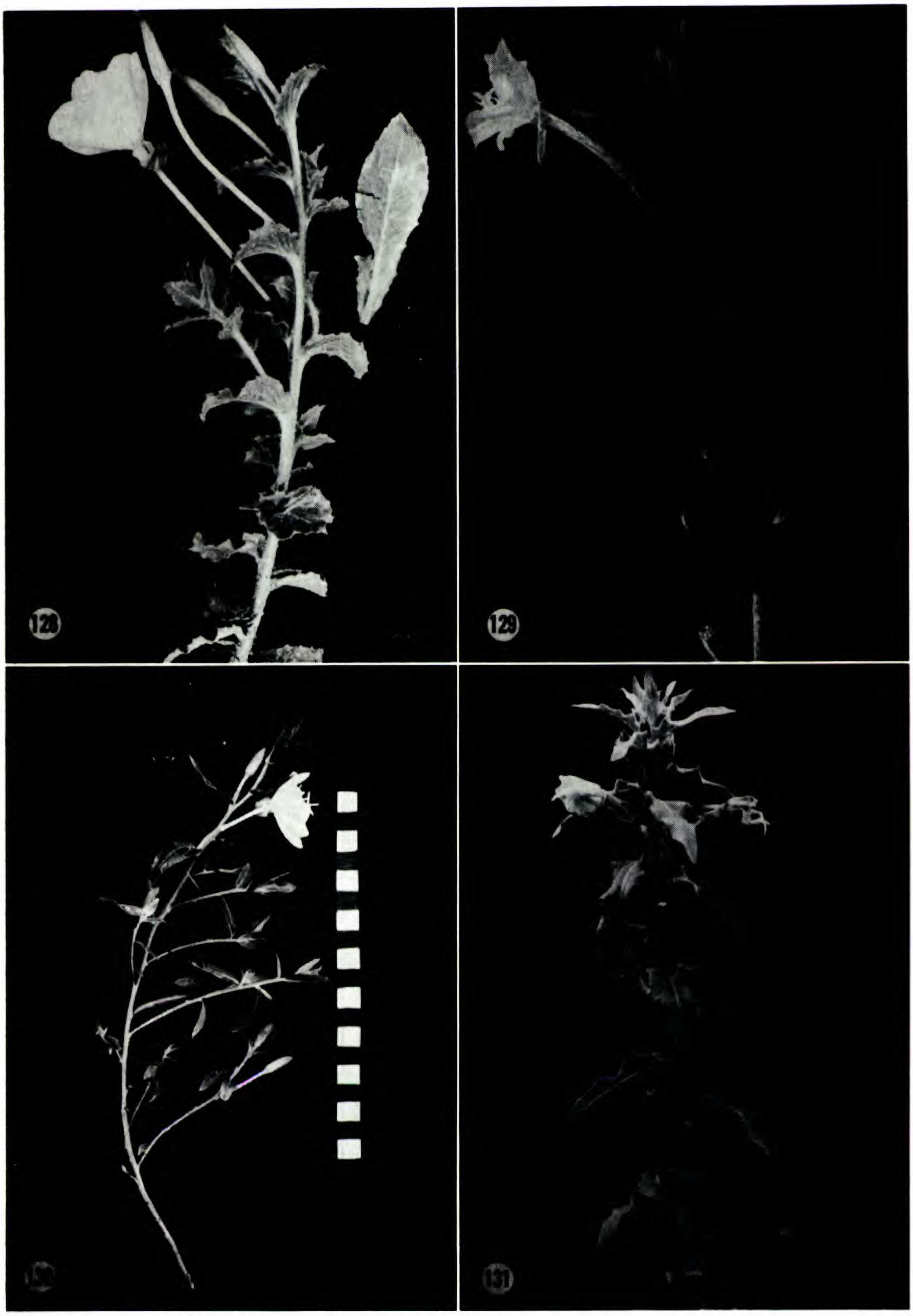
Since no fewer than four different chromosomal complexes are involved in the origin of *O. sandiana*—those from *O. peruana*, *O. versicolor*, *O. longituba*, and *O. scabra*—it is not surprising that it includes a wide array of different forms. The major role is, however, played by *O. versicolor* and *O. scabra*. It has not proven possible to divide this species into useful infraspecific categories, however.

Even the variation in single populations is astounding at times. Growing next to plants which are more or less intermediate between *O. versicolor* and *O. scabra* occur others which resemble one or the other species more strongly. In addition to these, there occur plants which clearly show characteristics of *O. longituba*, such as a long floral tube and flowers that overtop the shoot apex. At other places, principally in the Bolivian portion of the range, the influence of *O. longituba* is noticeably stronger. It can be assumed that the genomes of this north-Argentinian species has introgressed into *O. sandiana* by way of *O. tarijensis* and *O. recurva*, or even by *O. elongata* and *O. pseudoelongata* (series *Clelandia*), and that in passing northward the influence of the *longituba*-complex becomes less and less.

The chromosomal complexes that occur in *O. sandiana* seem rarely to occur in unaltered form, and evidently mechanisms have operated to intermix the genomes of the species involved in its origin. It seems clear that whatever the pairing relationships of the chromosomes in the complex heterozygote that the genes determining the major phenotypic characteristics have to some extent been substituted for in the course of evolution. Moreover, additional reciprocal translocations between nonhomologous chromosomes could lead to a breaking-up of the ring of 14 and the origin of unstable chromosomal complexes.

Since *O. versicolor* and *O. scabra* are chromosomally homozygous throughout the entire range of *O. sandiana*, it seems logical to assume occasional backcrossing between the complex heterozygous derivative and its parents, the plants involved being more or less typical of the species or perhaps already altered by hybridization themselves. This would inevitably lead to the production of plants that are not strictly intermediate between *O. versicolor* and *O. scabra*. Between a complex heterozygote and the species that participated in its formation there are usually no barriers to hybridization or recombination.

Within the very different appearing individuals of this species spontaneous hybrids with small rings of chromosomes or bivalents arise infrequently. From this it may be concluded that among the variety of end arrangements that presumably exist in at least many populations of the species, there is a sort of



FIGURES 128–131. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—128. *O. longiflora* subsp. *grandiflora* (Argentina, Corrientes, *Krapovickas & Cristóbal 11293*).—129. *O. longiflora* subsp. *longiflora* (Uruguay, Colonia, *Santarius 73*).—130. *O. catharinensis* (Brazil, Santa Catarina, *Conrad & Dietrich 13*).—131. *O. indecora* subsp. *indecora* (Uruguay, Florida, *Santarius 206*).

equality or balance between them so that hybrids always have a ring of 14 chromosomes, even though it may be formed in various ways and through the association of various combinations of chromosome ends. If this equality of genomes is disturbed, apparently there is a selection for end arrangements that will lead predictably to the consistent formation of plants with a ring of 14 within the population.

13. **Oenothera nana** Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 143. 1874. —FIGS. 1, 24, 120, 203–204.

O. punae sensu Munz & Johnston, Contr. Gray Herb. 75: 19. 1925, pro parte.

Annual to perhaps perennial plants, growing only as a rosette, but often with a central shoot up to 10 cm long and short, prostrate side branches. Plants either exclusively and densely strigillose or, especially in the inflorescence, with an admixture of appressed long-villous pubescence. Leaves linear to very narrowly elliptic, acute, the lower ones gradually narrowed to the petiole, the upper ones ± sessile, narrowly cuneate to acute at the base; leaves plane or ± undulate at the margins, irregularly serrate with blunt or acute teeth, often flecked with dark brown or black. Flowers formed in the axils of the rosette leaves. Floral tube 4–10(–15) mm long. Buds oblong to broadly oblong or broadly elliptic to rotund in outline, green to yellowish, often flushed with red, 2–4 mm long, 2–3 mm thick; apices of the sepals ca. 0.5 mm long, erect or divergent. Petals very broadly obovate, rounded or retuse, yellow, often flushed with red, 3–5 mm long. Anthers 2–3 mm long. Filaments 3–4 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 6–13 mm long. Stigma lobes 1.5–2 mm long. Ovary 5–10 mm long. Capsule narrowly lanceolate to lanceolate in outline, 1–2 cm long, 3–4 mm thick, standing at right angles to the stem, often arched downward at the apex. Seeds 0.7–1.1(–1.5) mm long, 0.4–0.5(–0.8) mm thick, broadly elliptic to rotund, rarely obtusely angled, light to dark brown, often with darker flecks. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: Peru, Chile, and Bolivia, December–April; Argentina, December–March.

Type: Argentina, Prov. Catamarca, sandy alpine valleys between Nacimientos and Laguna Blanca, end of Jan. 1870, *P. G. Lorentz 467* (GOET, holotype; CORD, isotype).

Distribution (Fig. 232): Andes from the departments of Puno and Arequipa in Peru, just touching northernmost Chile, and through Bolivia to the province of San Juan in Argentina, 2,500–4,700 m elevation.

Specimens examined from cultivated plants:

PERU. PUNO: Sandy places 2 km SE of Zepita, 3,820 m, *Santarius 2035, 2036*, 2037–2039* (DUSS; *2039* also CTES, M; *2035, 2038, 2039* also MO). Sandy slopes above Chimu, 8 km SE of Puno on road to Chucuito, 3,900 m, *Santarius 2045* (CTES, DUSS, M, MO); 4,000 m, *Santarius 2046* pro parte, *2049–2053, 2055** pro parte, *2056*, 2058** (DUSS; 2051, 2055 also CTES; *2046, 2051, 2055, 2056, 2058* also M, MO).

BOLIVIA. POTOSÍ: Waste places in E part of Potosí, 4,100 m, *Santarius 1961, 1966–1969* (DUSS; *1966* also CTES, M, MO).

ARGENTINA. JUJUY: Puna vegetation, 1 km S of Abra Pampa, *Santarius 1886** pro parte (DUSS, M, MO). Sandy places in puna vegetation, 3 km E of La Quiaca on road to Yavi, 3,550 m, *Santarius 1888*, 1889, 1890, 1892–1897, 1899, 1900–1904, 1905*, 1906–1908* (DUSS; *1895, 1905* also CTES, M; *1888, 1895, 1897, 1905* also MO). Sandy places 4 km W of Yavi, 3,600 m, *Santarius 1910*, 1911, 1912, 1914–1922* (DUSS; *1910* also CTES, M; *1910, 1916* also MO). CATAMARCA: Sierra de Ambato, top of Cerro Manchado, 4,300–4,450 m, *Hunziker 72-1345** (DUSS, MO).

Additional specimens examined:

PERU. AREQUIPA: Chiguate, 2,700 m, *N.N. in 1954* (RSA). MOQUEGUA: Carumas near Volcán Ticsaní, 4,000 m, *Weberbauer 7324* (F, GH, POM, S, US). PUNO: Sta. Lucia near Puno, ca. 4,700 m, *Sharpe 137* (K). Between Ilave and Mazo Cruz, 3,850 m, *Tovar 5294* (USM). Occa Pampa near Huancané, ca. 3,800 m, *Shepard 86* (GH). Vilque, 3,750 m, *Iltis & Ugent 1354* (K).

CHILE. TARAPACÁ: Putre near Arica, 4,000 m, *N.N. in 1948* (K). Caritaya near Tranque, 3,600 m, *Behn 19602* (CONC).

BOLIVIA. LA PAZ: 3,900 m, *Buchtien 644* (NY, US), *644a* pro parte (US), 3,700 m, *Buchtien 654* (GH, NY). Guaqui, 3,900 m, *Asplund 5983* (US). Guayamarca near Caño, *D'Orbigny 1930* (P). Pacajes, Ulloma, 3,800 m, *Asplund 4467* (UPS). Near Corocoro, 4,200 m, *Asplund 4467* (UPS). COCHABAMBA: Cona Cona station on the line from Oruro to Cochabamba, ca. 3,960 m, *Brooke 5214* pro parte (BM). Potosí, Uyuni, 3,700 m, *Asplund in 1921* (US). TARIJA: Between Quebrada and Salitre, ca. 4,000 m, *Fries 1028* (S).

ARGENTINA. JUJUY: Tumbaya, Abra de Pibes, 4,000–4,050 m, *Sleumer 3274* (LIL). Humahuaca, Tres Cruces, 3,700 m, *Cabrera et al. 15243* pro parte (LP); *Venturi 10088* (US). Dep. Cochinoca, Laguna Tres Cruces, 3,700 m, *Claren 11678* (CORD). Humahuaca, Cerro La Soldad, 3,500 m, *Venturi 9010* (US). Sta. Catalina, 3,400–4,300 m, *Kurtz 11454* (CORD, POM); 3,650 m, *Claren in 1901* (S). Dep. Tilcara, Yala de Monte Carmelo, 2,900 m, *Fabris 6402* (BAA, MO). Moreno, 3,500 m, *Fries 938* (S). Yaví, 3,600 m, *Sleumer 3603* (LIL); 3,500 m, *Fries 938a* (S); *Cabrera 21470* (LP). Susques, 3,700 m, *Cabrera 8750* (LP); *Castellanos in 1927* (POM). Sierra de Aguilar, Vicuñayua, 3,900 m, *Schwabe 514* (BAB). Citeara, 3,000 m, *Venturi 6512* (US). SALTA: El Alisal, 2,800 m, *Rodríguez 1292* (LIL, POM). La Laguna, Cerro Cajón, 3,900 m, *Rodríguez 1292* (SI). Montañas, *Rodríguez 1525* (BA). San Carlos, Cerro de Cachi, 4,400 m, *Venturi 6948* (US). TUCUMÁN: Cerro Muñoz near Tafí, *Fabris 1517* (LP); 4,000 m, *Lillo 4188* (GH, LIL, POM), 3,900 m, *4223, 7409* (LIL). Peak of Calchaquies, 4,200 m, *Lillo 5516* (LIL, MO, POM). Tafí, Infiernillo, *Castillon 3185* (LIL). Tafí, Las Lagunas, 4,000 m, *N.N. in 1926* (LIL 80079). Cerro Negrito, 4,100 m, *Sparre 6121* (LIL), 4,100 m, *6059* (LIL), 4,300 m, *8610* (LIL). Peak of Chaquivil, *Olea 248* (NY). Distr. Cabalao del Valle, Cajón, 3,900 m, *Schretter 4791* (LIL). CATAMARCA: Cerro Yutuyaco, 3,600–3,800 m, *Sleumer 2724* (LIL). Río Potrero near Choyana, 3,600 m, *Sleumer 1926* (LIL). Tinogasta, 3,100 m, *Schmitz 6251* (LIL). From La Coipita to Vallecito near Tinogasta, 3,100 m, *Schreiter 6251* (LIL). Sierra de Ambato, Cerro Manchado, 4,300–4,450 m, *Hunziker 20853* (CORD), 3,500 m, *20983* (CORD), 4,000–4,100 m, *20010* (CORD), 3,300–3,400 m, *Hunziker 19766* (CORD). LA RIOJA: Sierra de Famatima, Vega del Real Viejo, *Kurtz 14780* (CORD). SAN JUAN: Cerro Tronador, Cuesta Las Casitas, *Spegazzini 212* pro parte (BAB).

The species, which has been known for a long time in the literature and in the herbarium as *O. nana*, *O. punae*, or *O. kuntziana*, is made up of two different elements. To the first belong plants with two chromosomal complexes from series *Renneria*, and this group includes the type of *O. nana*. To the second group belong plants in which are combined one genome from series *Renneria* and one from series *Allochroa*. These plants belong by definition to subsect. *Clelandia*. For them, the name *O. punae* is to be used.

It is clear that the complex heterozygous *O. nana*, with its very condensed habit, has been derived from plants of normal stature in the process of adaptation to the extreme conditions at the high elevations where it occurs. I have already referred to *O. lasiocarpa* as a transitional species, and there are plants in *O. nana* which have some of the characteristics of that species.

On account of the extremely condensed habit of *O. nana*, a complex mode of adaptation that alters the expression of many characteristics, it is difficult to analyze the origin of this species. The analysis of hybrids with species of normal stature has revealed, however, the probable influence of *O. peruana, O. versicolor, O. lasiocarpa*, and *O. scabra* each with varying expression of their features in *O. nana*. The influence of *O. versicolor* and *O. lasiocarpa* appears to be stronger in the southern part of the range of *O. nana*, and that of *O. peruana* and *O. scabra* seems stronger in the north.

The individuals in a population are rarely uniform, but vary in the same way as has been discussed for *O. sandiana*. The situation is made still more complex by the fact that *O. nana* occurs together with *O. punae* at many localities, and their chromosomal complexes are essentially interchangeable with one another; see also the remarks on p. 611 in this connection.

The nanism of *O. nana*, its most prominent characteristic, can be manifested in various ways. Both complexes can have the dominant traits for normal size expressed, or one complex can be dominant and the other intermediate or recessive.

Series II. ALLOCHROA

Oenothera sect. **Oenothera** subsect. **Munzia** series **Allochroa** (Fischer & Meyer) Dietrich, comb. nov. Based on *Oenothera* sect. *Allochroa* Fischer & Meyer, Ind. Sem. Hort. Petrop. 2: 44. 1836.

Onagra sensu Moench, Meth. Pl. 1: 675. 1794, pro parte; Suppl. Meth. Pl. 2: 287. 1802, pro parte.
Oenothera sect. *Onagra* Séringe ex DC., Prodr. 4: 46. 1828, pro parte.
Oenothera sensu Spach, Nouv. Ann. Mus. Hist. Nat. 341. 1835, pro parte.
Oenothera sensu Raimann, in Engler & Prantl, Nat. Pflanzenfam. III, 7: 214. 1893, pro parte.
Raimannia sensu Sprague & Riley, Bull. Misc. Infor. 1921: 200. 1921, pro parte.
Oenothera § *Raimannia* sensu Munz & Johnston, Contr. Gray Herb. 75: 16. 1925, pro parte.
Oenothera subgen. *Raimannia* Munz, Physis 11: 279. 1933, pro parte; Amer. J. Bot. 22: 645. 1935, pro parte; Revista Univ. (Santiago) 22: 261. 1937, pro parte; Comun. Bot. Mus. Hist. Nat. Montevideo 1(10): 26. 1943.
Oenothera subgen. *Raimannia* sect. *Raimannia* Munz, North Amer. Fl., ser. 2, 5: 105. 1965, pro parte.

Erect annual or biennial herbs, rarely prostrate, forming a rosette or the stem elongating soon after the development of a few basal leaves, unbranched or with a branched main stem and ascending branches from the rosette which either arch outward in ascending or rise sharply and abruptly; plants 0.5–15 dm tall, rarely even taller. Stems more slender than in series *Renneria*, 2 to at most 10 mm thick. Plants (1) exclusively strigillose; (2) densely to sparsely strigillose, densely to sparsely long- and short-villous, the hairs mostly appressed, and densely to sparsely glandular-pubescent; (3) very densely to sparsely long- and short-villous and densely to sparsely glandular-pubescent; or (4) densely short-villous and densely glandular-pubescent. Rosette leaves linear to oblong, very narrowly oblanceolate to oblanceolate or narrowly elliptic, long- or short-acute, sessile and narrowly cuneate to truncate at the base or gradually narrowed to the petiole, 8–25 cm long, 0.4–3.5 cm wide; cauline leaves linear to oblong, very narrowly elliptic to elliptic or narrowly lanceolate to narrowly ovate, acute, sessile, narrowly cuneate to truncate at the base, 2–20 cm long, 0.2–3 cm wide; bracts linear to broadly oblong, narrowly elliptic to elliptic or narrowly lanceolate to ovate, acute to obtuse, rarely almost rounded, sessile, acute to subcordate at the base, 2–10 cm long, 0.2–2.5 cm wide; leaves mostly irregularly and distantly serrate with dull teeth, occasionally very coarsely serrate or doubly serrate (*O. coquimbensis*), plane or evidently to very slightly undulate along the edges. Inflorescence unbranched or branched, lax; flowers erect in anthesis, one opening each day. Floral tube 0.5–13 cm long. Buds oblong, elliptic to broadly elliptic or narrowly lanceolate to narrowly ovate in outline, 0.3–3.5 cm long, 2–11 mm thick, often with red stripes at the junction with the floral tube. Sepals green or yellowish green, often flushed with red, sometimes densely to sparsely flecked with dark red; apices of the sepals 0.5–4 mm long, erect, spreading, or hornlike. Petals obovate to very broadly obovate, rarely elliptic to broadly elliptic, rounded or retuse, 0.3–5 cm long, yellow to bright yellow, sometimes with a red basal spot. Ovary 1–2.5 cm long. Capsule linear to narrowly oblong in outline, terete, rarely slightly enlarged in the upper third or tapering at both ends and appearing short-petiolate, projecting obliquely from the stem, straight or slightly curved, (1.5–)2–6 cm long, 2–5 mm thick, not fused with the bract; valves curving outward or inward after the capsule dehisces, occasionally spreading. Seeds 1–2 mm long, 0.4–1.1 mm thick, narrowly elliptic to rotund in outline, light or dark brown to almost black. Self-compatible; chromosomal homozygotes or self-pollinating complex heterozygotes, rarely outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents, ring of 14 or intermediate configurations at meiotic metaphase I).

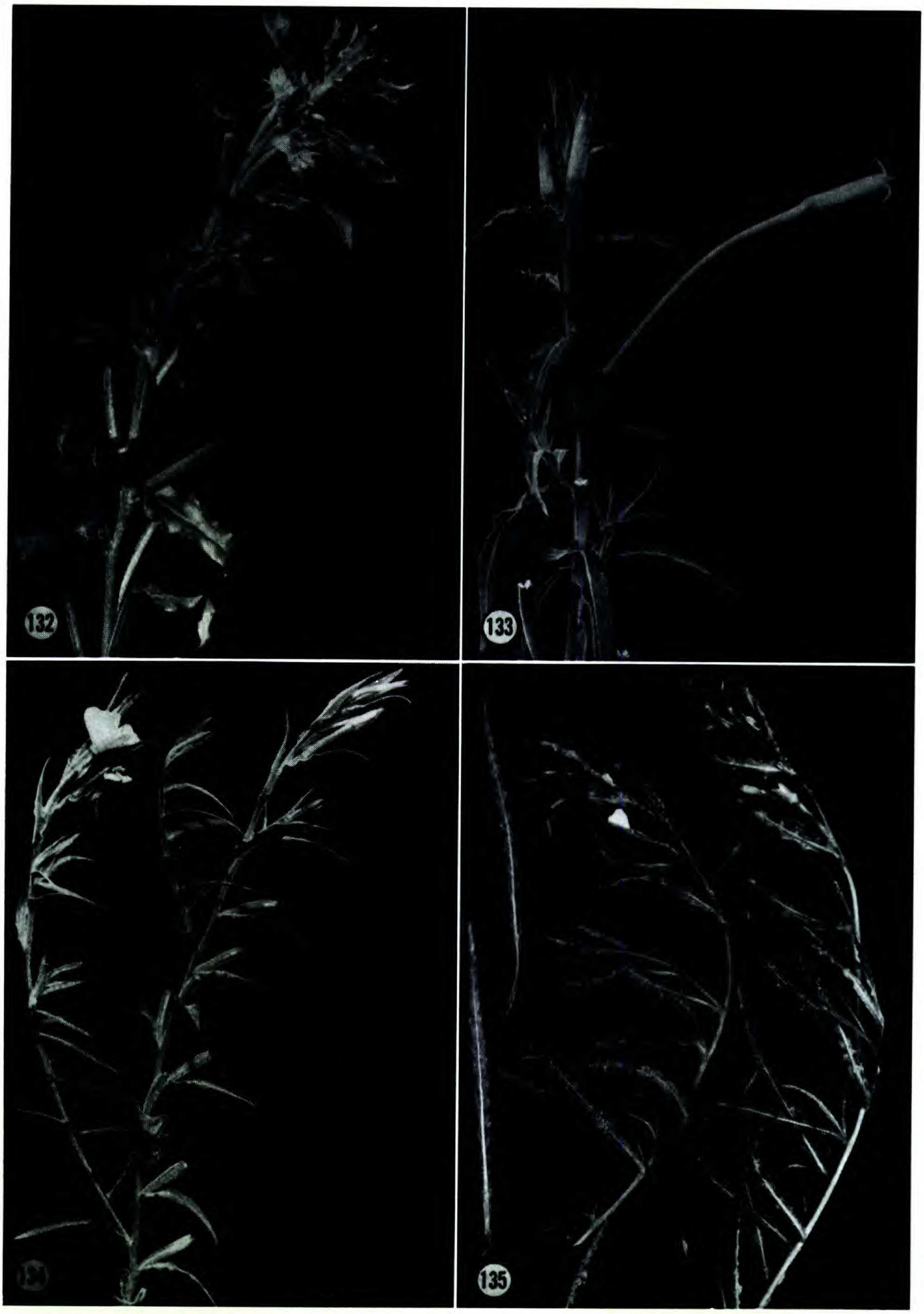
Type species: *Oenothera mollissima* L.

Distribution (Fig. 7): These are predominantly plants of relatively low elevations from sea level upward; ascending to 3,200 m elevation in the Andes (*O. affinis, O. arequipensis, O. featherstonei, O. nocturna, O. odorata, O. verrucosa*). In Brazil, the plants occur in Guanabara, southern Minas Geraís, and in São Paulo to Rio Grande do Sul. They occur throughout Uruguay and in all provinces of Argentina as far as Río Gallegos in Patagonia, extending northward to Tarija in Bolivia. West of the Andes, they range in Chile from the provinces of Atacama to Magellanes, and in the coastal deserts and semideserts from the department of La Libertad in Peru to Valparaíso in northern Chile. In Peru they ascend into the mountains along river valleys to 3,200 m elevation.

If the isolated stations that occur up to 3,200 m elevation in the Andes are disregarded, most species of this series are inhabitants of the broad plains of Argentina and the coastal regions on both the Atlantic and Pacific shores of southern South America, and the lowermost slopes of the mountains.

All species have more slender stems and are more graceful than the sturdy, thick-stemmed species of series *Renneria*. Important differences from that series are the laxer inflorescences, erect flowers, and obliquely divergent capsules.

Most of the species of series *Allochroa* form a rosette, like the majority of those of series *Renneria*. Among the chromosomally homozygous species, only



FIGURES 132–135. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—132. *O. indecora* subsp. ***bonariensis*** (Argentina, Buenos Aires, *Santarius 278*).—133. *O. affinis* (Argentina, Tucumán, *Santarius 1801*).—134. *O. mollissima* (Uruguay, Montevideo, *Santarius 42*).—135. *O. rivadaviae* (Argentina, Chubut, *Santarius 924*).

O. affinis, *O. catharinensis*, *O. coquimbensis*, and *O. verrucosa* form no rosette; whereas among the complex heterozygotes, no rosette is formed by those which incorporate a genome from *O. affinis*: namely, *O. mollissima*, *O. montevidensis*, and *O. picensis*.

14. **Oenothera mendocinensis** Gillies ex Hooker & Arnott, Bot. Misc. 3: 310. 1833.—FIGS. 35–36, 121, 174, 210.

O. odorata sensu Hicken, Physis 2: 110. 1916.

Raimannia mendocinensis (Gillies ex Hooker & Arnott) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.

Oenothera argentinae H. Lév. & Thell. var. *camptotricha* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherlands, Rotterdam, Maashaven meal factory, 10 Sep. 1920, *A. W. Kloos* (BAS).

O. indecora sensu Munz, Physis 11: 281. 1933, pro parte; Amer. J. Bot. 22: 658. 1935, pro parte.

Erect annual herb, forming a rosette, unbranched or with a branched main stem and widely arching or obliquely ascending side branches arising from the rosette, 3–6 dm tall. Plants either exclusively and densely strigillose or densely to sparely strigillose and densely to sparely villous, but often strigillose only near the base. Rosette leaves linear, acute, narrowed to the petiole, 7–14 cm long, 3–5 mm wide; cauline leaves linear, acute, 3–6 cm long, 2–4 mm wide; bracts linear, acute, truncate at the base, sessile, 3–5 cm long, 1–3 mm wide, mostly somewhat longer than the capsules or ± the same length; leaves plane or slightly undulate at the margins, irregularly serrate. Inflorescence branched. Floral tube 0.5–1.5 cm long. Buds oblong to elliptic in outline, gray green, often flushed with red, 4–9 mm long, 2–4 mm thick; apices of the sepals erect, 0.5–1 mm long. Petals very broadly obovate, 0.5–1 cm long. Anthers 2.5–5 mm long. Filaments 3–5 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 8–21 mm long. Stigma lobes 2–3.5 mm long. Ovary 1.2–1.8 cm long. Capsule (2–)3–6 cm long, 2–3 mm thick. Seeds elliptic in outline, light brown, (1–)1.2–1.8 mm long, 0.5–0.7 mm thick. Self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: October–March.

Lectotype: Argentina, Prov. Mendoza, between Las Chacayes and Melocotón, foot of the Andes of Mendoza, (1824?), *Gillies* (K, POM photograph; a photograph of isolectotype at E, from Herb. GL). Two sheets of the type collection are in K, both mixed with *O. indecora* (one collected by Charles Darwin at Bahía Blanca in 1832). Because *O. indecora* does not occur in the province of Mendoza and because it cannot be determined with certainty which plants the labels correspond to, only one branch has been selected as lectotype. For this branch, the correspondence of the plant with the label is clear.

Distribution (Fig. 226): Occurs only at low elevations, ascending to 1,500 m in the Andean foothills of Mendoza. The range includes the following provinces of Argentina: Mendoza, San Luis, Córdoba, Buenos Aires, La Pampa, Río Negro, Chubut, and Santa Cruz.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Dunes ca. 2 km SE of Argerich, 37 km W of Bahía Blanca, *Santarius 402**, *411**, *412*, *415**, *417*, *420**, *421**, *423*, *425*, *431**, *433*, *435**, *438*, *442**, *443*, *445*, *448* (DUSS; *402*, *420*, *421* also CTES; *402*, *415*, *420*, *421*, *442* also M; *402*, *420*, *421*, *425* also MO). Dunes along road from Villa del Mar to Ruta 229, ca. 5 km NNW of Punta Alta, *Santarius 518**, *521*, *529*, *533**, *536* (DUSS; *533* also M; *521*, *533* also MO). CHUBUT: Dunes SE of Puerto Madryn, *Santarius 1354**, *1356**, *1358*, *1361*, *1367*, *1371*, *1374**, *1378*, *1382*, *1390* (DUSS; *1354*, *1374* also CTES; *1354*, *1356*, *1374* also M; *1354*, *1371*, *1374* also MO).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: Daireaux, *Parodi 13163* (BAA). Monte Veloz, *Parodi 12238* (BAA). General Villegas, dunes near Bunge, *Cabrera 5703* (LP). Between Piedritas and Cañada Seca near General Villegas, *Hunziker 12826* (CORD, MO). Salliquelo, Est. "Los Gorros" near Pellegrini, *Cabrera 8012*, (F, GH). Dunes near Pellegrini, *Cabrera 6955* (LP). Punta Alta, *O'Donell 1513* (LIL). Colonel Dorrego, Monte Hermoso, *Erettowi 2607* (MO). From Urdampilleta to Piravano on Ruta 205 near Bolívar, *Vervoorst 5437* (BAB). 25 km SE Carmen de Patagones, *Fabris & Schwabe 5001* (LP). Río Negro near Carmen de Patagones, *Hunziker 414* (CORD); *Meyer 6991* (LIL). Between Bahía San Blas and San Blas, *Ameghino in 1903* (POM). Villarino near Bahía Blanca, *Correa 2387* (BAB); *Boelcke 11788* (BAA, MO, SI). Ruta 22, *Puerto 11552* (MVFA). Argerich near Villarino, *Parodi 13799* (BAA, MO). Agustina near Junín, *Cabrera 6560* (F, SP, NY). CÓRDOBA: Near Pacheco de Melo, road to Laboulaye, *Hunziker 12768* (CORD, MO), *12779* (CORD). Between Laboulaye and Salguero, *Hunziker 12810* (CORD, MO, RSA). Sierra Chica, La Redución, *Burkart 17325* (SI). Laguna Brava, 400 m, *King 319* (BM). Quinta Soriano N of Bajo Grande near Córdoba, *Kurtz 16128* (CORD, MO). Between Est. S. Miguel and Rufino near Santa Fé, *Spegazzini 6915* pro parte (BAB). Between Rufino and La Cesira, *Hunziker 12853* (RSA). Sierra Ochoa, *Stuckert 13562* (G). Dep. Unión, La Carlota, *Hunziker 11206* (CORD, MO). Est. La Mascota near Ballesteros, *Hunziker 12751* (CORD, RSA). SAN LUIS: Laguna near Sayape, *Castellanos in 1949* (LIL). Pedernera on Ruta 148, 10 km S Villa Mercedes, 510 m, *Anderson 1338* (LP). Villa Mercedes, *Corradi 4832* (SI). Between Villa Mercedes and Juan Jorba on Ruta 8, *Hunziker 13170* (CORD, RSA). Near Esquina on Ruta 7, between San Luis and E. Lobos, *Hunziker 13123* (CORD). Dep. General Pederrera, on Ruta 148 between Laraisse and El Durazno, 500 m, *Hunziker 15977* (CORD). Nueva Escocia, *Burkart 10840*, *10808* (LIL, SI). LA PAMPA: Guatraché, *Viguier 94* (BAB). General Pico, *Burkart 9919* (LIL, SI). General Acha, *Orbea in 1953* (SI, US); *Burkart 19205* (SI). Between General Acha and Santa Rosa, *Troncoso in 1959* (SI). General Lagos (SI-4856). Laguna La Asturiana, *Bacigalupo in 1959* (P, SI). La Pampa, *Monticelli 39* (SI). MENDOZA: Las Heras, La Crucesita, *Ruiz Leal 5378* (Leal). Mina Atalu, *Ruiz Leal 3328* (Leal). Dep. Tunuyán, La Piedra Rajada, *Ruiz Leal 1707* (Leal). Tupungato, road to Est. Silva, 1,500 m, *Cáceres 6* (LIL, NY). 10 km W Campo de Los Andes, 1,500 m, *Araque & Barkley 20Mz179* (LIL). Tupungato, *Ruiz Leal 2784a* (LIL). Dep. San Carlos, Est. Viluco, *Torres 36* (SI). Mendoza, *Jörgensen 131* (BAB, C). RÍO NEGRO: S. Antonio, *Guernant in 1910* (LIL). General Roca, 250–360 m, *Fischer 86* (BM, F, GH, K, MO, NY, SI, US). Dep. General Roca, banks of Río Negro near J. J. Gomez, *Krapovickas et al.* (CTES). Río Negro, *Berg 98* (CORD); *N. N. 88 in 1874* (LE). SANTA CRUZ: Territory of Santa Cruz, *Ameghino 32* (BA).

Specimens from outside of South America:

NETHERLANDS. Rotterdam, 1902, *Jansen & Wachter 13286* (L); 1931, *Kern & Reichgelt 12181* (L).

GERMANY. Emmerich on Rhine River, 1931, *Kern & Reichgelt 5064* (L).

Its small flowers, very small leaves, mostly long and narrow fruits, and strigillose pubescence set off *O. mendocinensis* as an isolated species. On the basis of the pubescence, it might be regarded as the least specialized species of the series, since it is the only chromosomally homozygous member of series *Allochroa* which has retained this characteristic of the members of series *Renneria*. On account of its slender habit and small flowers, *O. mendocinensis* has been included incorrectly in the synonymy of *O. indecora*, on the assumption that a marked similarity between these species indicates a close relationship. The hybrid between *Santarius 405* (*O. mendocinensis*) and *O. argentinae "Erlangen"*

(= *O. indecora* subsp. *bonariensis*) formed 7 bivalents at meiotic metaphase I, from which it cannot be inferred, however, that *O. mendocinensis* and *O. indecora* are closely related, as discussed in the introduction.

Oenothera mendocinensis is closely related to *O. odorata*, judged from their close similarity in habit, leaf form, and characteristics of the capsule and seeds. They have probably been derived from a common ancestor (Fig. 8), a suggestion which is consistent with their ranges.

It appears likely that the more generalized ancestral forms in series *Allochroa*—the closest living equivalents of which may be *O. mendocinensis* and *O. odorata*—were probably derived from generalized members of series *Renneria* in a center which on the basis of present-day distributions would appear to have been in and about the province of Mendoza. They then migrated to the south and southeast. The more advanced species (*O. indecora, O. ravenii, O. longiflora, O. affinis*), on the other hand, may have originated farther north, in the region of the provinces of Catamarca and Tucumán, and then spread predominantly toward the east and northeast and the region of the Chaco (Fig. 8).

15. **Oenothera odorata** Jacq., Icon. Pl. Rar. 3: *tab. 456.* 1795; Suppl. Coll. Bot. 5: 107. 1796.—FIGS. 37–40, 122–123, 175, 211.

Onagra undulata Moench, Suppl. Meth. Pl.: 287. 1802. TYPE: The herbarium of Moench apparently no longer exists.

Oenothera undulata W. T. Aiton, Hortus Kew. 2: 342. 1811. TYPE: Seeds from Port Desire, Argentina, 1790, cultivated at Kew (not seen).

O. odorata var. *virescens* Séringe in DC., Prodr. 3: 48. 1828. LECTOTYPE: Hort. parisiensis, 1816, *M. Brun in 1824* (G-DC). Grown from seed from the same source as the type of the species.

O. odorata var. *glaucescens* Séringe in DC., Prodr. 3: 48. 1828. LECTOTYPE: 28 August, *h.h.* (G-DC).

O. odoratissima Tausch, Flora 22: 557. 1839. LECTOTYPE: Cultivated in botanical garden, Herb. *V. Kosteletzky* (PRC, POM photograph); Munz, Amer. J. Bot. 22: 661. 1935.

O. mollissima sensu Hooker & Arnott, Bot. Beech. Voy. 23. 1841.

O. ibari Philippi, Anales Univ. Chile 84: 633. 1893. LECTOTYPE: Argentina, Prov. Santa Cruz, Lago Argentino (Lago Santa Cruz), 30 Jan. 1879, *E. Ibar* (SGO, GH photograph).

O. odorata f. *glabrescens, media* and *undulata* Spegazzini, Revista Fac. Agron. Univ. Nac. La Plata: 520. 1898. TYPES: not located.

O. mollissima sensu Macloskie, Rep. Princeton Univ. Exped. Patagonia 8(5, 3): 613. 1905.

Onothera polymorpha H. Lév. race *odorata* (Jacq.) H. Lév., Monogr. Onoth. 363. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.

O. polymorpha race *odorata* var. *undulata* (W. T. Aiton) H. Lév., Monogr. Onoth. 363. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.

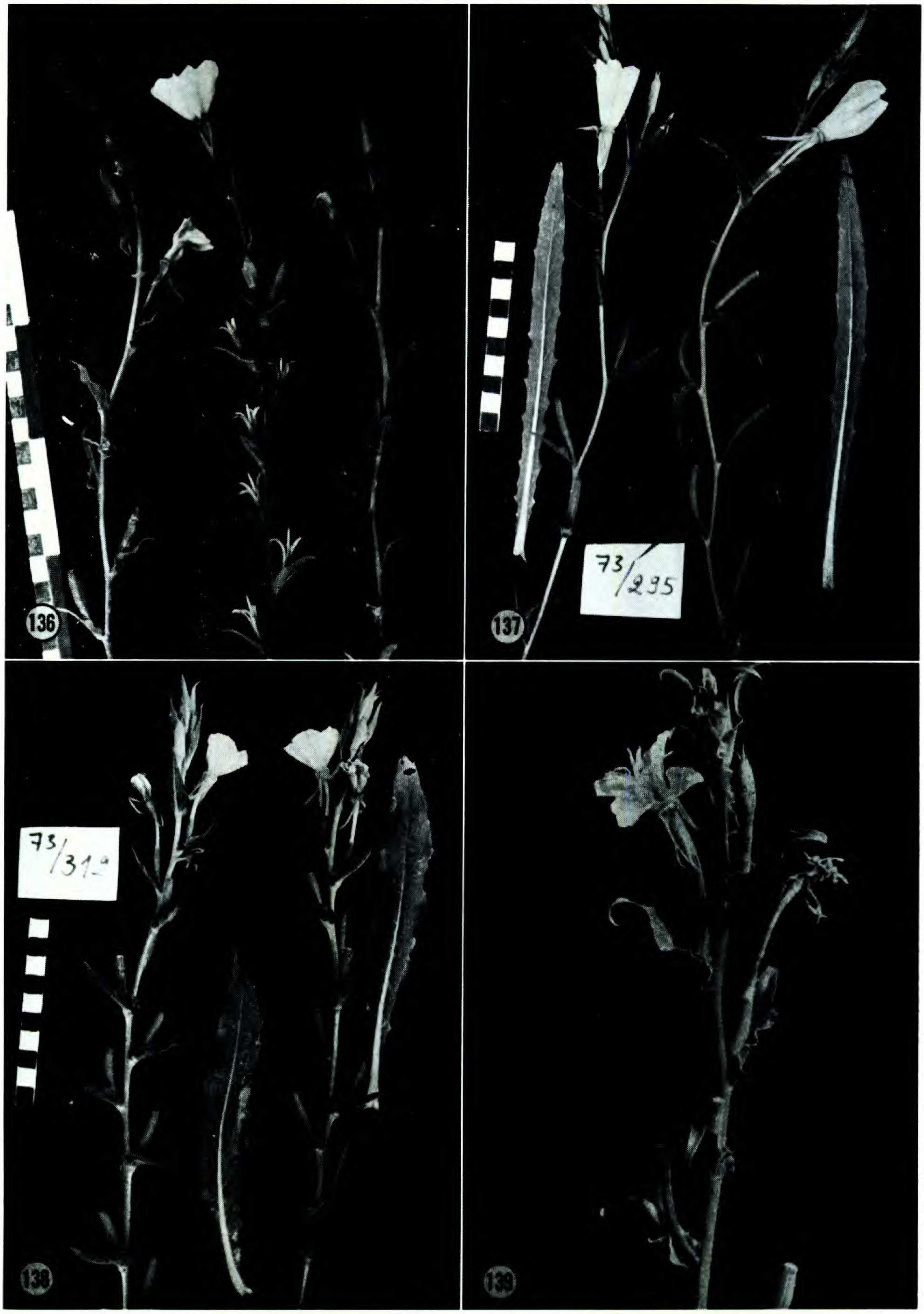
O. polymorpha race *propinqua* (Spach) H. Lév. var. *ibari* (Philippi) H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909.

Oenothera mollissima subsp. *odorata* (Jacq.) Thell., Mitt. Bot. Mus. Univ. Zürich 58: 390. 1912.

Raimannia odorata (Jacq.) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.

Oenothera stricta sensu Munz, Physis 11: 285. 1933, pro parte; Amer. J. Bot. 22: 661. 1935, pro parte.

Erect annual herb, forming a rosette or the stem elongating after the formation of a few basal leaves, unbranched or with a branched main stem and prostrate or widely arcuate-spreading to obliquely ascending side branches arising from the rosette, 2.5–8 dm tall. Plants densely or sparsely strigillose and densely



FIGURES 136–139. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—136. *O. stricta* subsp. *stricta* (Chile, Cautín, *Stubbe in 1960*).—137. *O. stricta* subsp. *altissima* (Argentina, Río Negro, *Santarius 798*).—138. *O. stricta* subsp. *argentinae* (Argentina, Buenos Aires, *Santarius 346*).—139. *O. bahia-blancae* (Argentina, Buenos Aires, *Santarius 457*).

or sparsely erect-villous or very densely to sparsely villous with erect long and short hairs, rarely sparsely glandular-pubescent. Rosette leaves linear to narrowly oblanceolate, acute, gradually narrowed to the petiole, 15–20 cm long, 0.5–1.5 cm wide; cauline leaves linear to very narrowly elliptic or narrowly lanceolate, acute, narrowly cuneate to acute at the base, short-petiolate or sessile, 5–18 cm long, 0.5–1.5 cm wide; bracts narrowly lanceolate to narrowly ovate, acute, truncate to subcordate at the base, 3–7 cm long, (0.3–)0.5–1.5 cm wide, shorter than, equal to, or longer than the capsule; leaves plane or the margins markedly to slightly undulate, irregularly serrulate. Inflorescence unbranched. Floral tube (1.5–)2–3 cm long. Buds lanceolate to narrowly ovate in outline, green or yellowish green, often flushed with red, 2–3 cm long, 0.5–1 cm thick; apices of the sepals erect, sharply divergent, or hornlike, 2–3 mm long. Petals very broadly obovate, retuse, 2–4.5 cm long. Anthers 9–14 mm long. Filaments 16–24 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, or long, the stigma held above the anthers at anthesis, 3.5–6.5 cm long. Stigma lobes 4–7 mm long. Ovary (1–)1.3–1.7 cm long. Capsule 3–5 cm long, 3–4 mm thick. Seeds elliptic in outline, light brown, 1.5–2 mm long, 0.5–0.8 mm thick. Self-compatible; autogamous in the complex heterozygotes, outcrossing in those chromosomal homozygotes in which the stigma is elevated above the anthers. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 14** or intermediate configurations at meiotic metaphase I). Flowering time: October–March.

Lectotype: Jacquin, Icon. Pl. Rar. 3: *tab. 456.* 1795. Cultivated in Vienna, seeds from Port Desire, ("Champion River"), Patagonia, Argentina, collected by Capt. Middleton and sent to Jacquin's son in 1793 by Sir Joseph Banks. Two specimens collected by Capt. Middleton are in the Forsyth Herbarium (NY), one from Port Desire, the other from Bay of San Dondo. Jacq., Coll. 107. 1796; Edwards, Bot. Reg. 2: *tab. 147.* 1816.

Distribution (Figs. 227, 242): Low elevations from sea level to 1,000 m altitude, in the provinces of Mendoza, Buenos Aires, Córdoba, La Pampa, Neuquén, Río Negro, Chubut, and Santa Cruz; ascending to 2,800 m elevation only in the cordilleras of Mendoza. In southern Chile it occurs only in the immediate vicinity of the border with Argentina.

Specimens examined from cultivated plants:

ARGENTINA. MENDOZA: Above El Peral, ca. 6 km NW of Tupungato, *Santarius 1574** (ring of 4, 5 bivalents) (DUSS, M, MO). Slopes of the Precordillera near Villavicencio, 2,500 m, *Santarius 1585, 1596*** (DUSS; *1585* also M, MO); 2,300 m, *Santarius 1614, 1624** (ring of 6, ring of 4, 2 bivalents), *1626, 1628, 1632, 1634* (ring of 10, 2 bivalents), *1637* (ring of 10, 2 bivalents) (DUSS; *1624* also CTES, M, MO); 1,750 m, *Santarius 1650* (ring of 6, 4 bivalents), *1651*** (DUSS; *1650* also MO). Dep. Las Heras, Caracoles de Villavicencio, *Hunziker 9073** (DUSS, M). BUENOS AIRES: Dunes near Mar del Plata, *Santarius 329** (ring of 4, 5 bivalents), *331, 333, 335, 336* (DUSS; *329* also CTES, M; *329, 331, 335* also MO). NEUQUÉN: Rocks ca. 500 m E of Piedra del Águila, 600 m, *Santarius 613* (ring of 8, 3 bivalents), *616* (ring of 8, 3 bivalents), *617*, 621*, 622, 624*, 625, 626, 627* (ring of 4, 5 bivalents), *629, 630*, 633*, 634, 635* (DUSS; *616, 617, 630* also CTES; *617, 621, 633* also M; *616, 617, 624, 626, 630* also MO). Río Limay at Ruta 237 ca. 75 km SSW of Piedra del Águila, *Santarius 644** (DUSS). Bank of Río Limay near Nahuel Huapí, 750 m, *Santarius 879**, 882***, *884* (DUSS). RÍO NEGRO: Bank of Río Limay at leaving of the Lago Nahuel Huapí, 750 m, *Santarius 887, 889, 892, 893**, 899, 902* (DUSS). Sandy and waste places along shore of

Lago Nahuel Huapí near the railroad station of San Carlos de Bariloche, 780 m, *Santarius 653* (ring of 12, 1 bivalent), *664* (ring of 4, 5 bivalents), *666, 668, 669* (ring of 10, 2 bivalents), *670** (ring of 10, 2 bivalents), *679* (ring of 6, 4 bivalents), *680** (ring of 6, 4 bivalents; ring of 8, 3 bivalents; ring of 10, 2 bivalents), *681, 682* (ring of 12, 1 bivalent), *686*, 688* (ring of 12, 1 bivalent), *689, 690, 693, 696*,*** (ring of 10, 2 bivalents), *697** (ring of 12, 1 bivalent), *701*, 702, 703*, 707*, 709, 713* (ring of 10, 2 bivalents), *714, 716*, 717*, 722* (ring of 4, 5 bivalents), *723* (ring of 8, 3 bivalents), *724*, 726*, 727, 732, 742, 746* (ring of 10, 2 bivalents), *749* (ring of 10, 2 bivalents), *751** (DUSS; *680, 716* also CTES; *653, 680, 689, 716* also M; *680, 686, 716, 746* also MO). E slope of Cerro Otto, 1 km W of Bariloche, 850 m, *Santarius 752*, 754, 755, 760* (ring of 10, 2 bivalents), *761* (ring of 6, ring of 4, 2 bivalents), *762, 765* (ring of 10, 2 bivalents), *766, 767** (ring of 10, 2 bivalents), *770, 771* (ring of 6, 4 bivalents), *777, 783*** (DUSS; *752* also CTES, M, MO); 950 m, *Santarius 788*, 790* (ring of 8, 3 bivalents) (DUSS). Slopes near Ruta 258, ca. 3 km N of Río Villegas, 67 km S of Bariloche, 700 m, *Santarius 800** (ring of 4, 5 bivalents), *801* (ring of 6, 4 bivalents), *802, 803, 806, 810**, 812, 814, 816, 819, 820* (ring of 8, 3 bivalents) (DUSS; *800* also M; *800, 801, 810* also CTES, MO). Estancia "San Ramón," W slopes at Río Limay, E of the bridge of Ruta 237 across the river, 750 m, *Santarius 854* (ring of 6, 4 bivalents; ring of 8, 3 bivalents; ring of 12, 1 bivalent), *866**, 868**, 872, 876, 878* (ring of 12, 1 bivalent) (DUSS; *878* also CTES, M, MO). CHUBUT: Sandy waste places in Villa Balneario Rada Tilly, ca. 14 km S of Comodoro Rivadavia, *Santarius 937* (ring of 12, 1 bivalent), *938* (ring of 12, 1 bivalent), *945* (ring of 12, 1 bivalent), *946, 947* (ring of 12, 1 bivalent), *948, 950* (ring of 12, 1 bivalent), *951, 953*, 954* (ring of 12, 1 bivalent), *957* (ring of 12, 1 bivalent), *958* (DUSS; *938, 950, 953, 957* also CTES, M, MO). SANTA CRUZ: Sandy places S of Puerto Deseado, at mouth of Río Deseado, *Santarius 959**, 961**, 963–967, 973**, 975, 979, 981**, 982**, 988* (ring of 8, 3 bivalents), *991, 994* (DUSS; *959* also CTES; *959, 982* also M; *959, 973, 981, 982* also MO). Sandy places in steppe with *Stipa*, 2 km NNE of Calafate at Lago Argentino, *Santarius 1162* (ring of 6, ring of 4, 2 bivalents; ring of 8, 3 bivalents), *1163, 1166, 1171* (ring of 4, 5 bivalents), *1175, 1179, 1182* (ring of 8, 3 bivalents), *1185* (ring of 6, 4 bivalents), *1190* (ring of 6, 4 bivalents), *1193* (ring of 6, ring of 4, 2 bivalents), *1194, 1196* (ring of 4, 5 bivalents) (DUSS; *1179* also M; *1175* also MO). Slope W of Arroyo Calafate, 350 m, *Santarius 1204** (ring of 8, 3 bivalents), *1206, 1208*, 1210, 1211* (DUSS; *1208* also M; *1208, 1210* also MO). Sandy places at E edge of Calafate, 200 m, *Santarius 1213*, 1216* (ring of 4, 5 bivalents), *1217, 1218* (ring of 8, 3 bivalents), *1220, 1228** (ring of 6, ring of 6, 1 bivalent), *1230** (ring of 4, 5 bivalents), *1233, 1239, 1241* (DUSS; *1213, 1230* also M; *1213, 1241* also MO). Near the airport of Calafate, 200 m, *Santarius 1245*, 1247, 1249, 1252* (DUSS; *1245* also CTES, M, MO). Stony and sandy places in the vicinity of Perito Moreno, 380 m, *Santarius 1257* (DUSS, MO). Lago Buenos Aires, at Río Los Antiguos W of Los Antiguos, 220 m, *Santarius 1322*, 1329* (ring of 12, 1 bivalent), *1331, 1332*, 1335* (ring of 10, 2 bivalents), *1336** (ring of 6, 4 bivalents; ring of 8, 3 bivalents; ring of 10, 2 bivalents) (DUSS; *1322, 1332, 1335*, also M; *1329, 1335, 1336* also CTES, MO).

CHILE. MAGELLANES: Ultima Esperanza near Salto de Paine, *Moore 990*** (DUSS, M, MO). 0–4 km E of Puente Lago Amarga, W of Lago Sarmiento, S of Lago Nordenskjold, *Santarius 1048**, 1049* (ring of 12, 1 bivalent), *1050* (ring of 12, 1 bivalent), *1052**, 1054, 1055, 1058*** (ring of 12, 1 bivalent), *1060, 1061* (ring of 12, 1 bivalent), *1064*** (DUSS; *1048, 1050* also CTES, M; *1048, 1050, 1058* also MO).

Representative specimens examined:

ARGENTINA. SAN JUAN: Calingasta, *Debenedetti* (SI-4859). MENDOZA: Villavicencio, 2,000 m, *Arque & Barkley in 1957* (LIL, NY); *Sleumer 469* (B, LIL), *Roig 5304* (CORD); *Ruiz Leal 1084* (Leal, LIL, POM); *Crovetto 9237* (BAB); *Wall in 1946* (S); *Mexia 04386* (GH, MO, UC); *Bartlett 19403* (GH, MICH, SI, US); *Senn 4443* (RSA). Los Hornillos, 2,600 m, *Barkley & Paci 240* (LIL, NY). Puente del Inca, 2,800 m, *Wall in 1946* (S). La Polvareda, 1850 m, *Palacios & Barkley 20 Mz331* (LIL, NY). Tunuyán, San Pablo, *Ruiz Leal 1812* (Leal, LIL, POM). Quebrada del Arroyo Manzano, 1,650 m, *Roig 4657* (CORD). Dep. Malalhue, Potimalal, 1,500 m, *Ruiz Leal 7492*, (Leal, LIL). Dep. Luján, El Carmelo, 2,000 m, *Cuezzo 2615* (LIL). Dep. San Rafael, Río Salado, Ciénaguita, *Rossi 294* (LIL). Dep. Tupungato, Canal Mártir near Toma, *Ruiz Leal 2794* (Leal, LIL, LP). Near San Pedro, *Gillies in 1824* (K). Paso Cruz, *Kuntze 59* (CORD, F). Dep. San Carlos, Quebrada Alvarado, *Covas 3492* (SI). Laguna Carrilauquen, *Kurtz 6109* (CORD, MO). Atuel Valley near El Sosneado, 1,600 m, *Böcher & Hjerting 881* (C). NEUQUÉN: Pulmaré, *Comber 388* (K). Between Catanlíl and Junín de los Andes at Río Aluminé, *Böcher et al. 1643* (C). Parque Nahuel Huapí, *De Barba 2106* (LIL, RSA); *Jacobsen 15* (POM). Manza near Zapala, *Ancibor 90245* (BAB).

Cohún-Có, *Comber 869* (K). Lago Huechulafquen, *O'Donell 2320* (LIL, NY, S, SI). Junction of Río Limay and Río Traful, *Cardini 46* (LIL). Cerro Lotena, 900 m, *Ammann 82* (F, M). Río Barrancas at Ruta 40 near Pehuenches, *Ancibor 90134* (BAB). San Martín de los Andes, *Dawson 1297* (BAA). Lago Lolog near San Martín de los Andes, *Scolnik 230* (RSA). RIO NEGRO: Parque Nahuel Huapí, *De Barba 750* (BM, LIL), *1462* (LIL, RSA); *Cardini 228* (US); *Giovanelli 13600* (BAB); *Bernicken in 1896* (LP), *Arnow 3761* (MO); *Fabris 1124* (BR); *Buchtien 1356* (AMD, BREM pro parte, GH pro parte, L, LE, LIL, LY, M, S, SI, US, W), *17* (POM). Banks of Río Negro near General Roca, *Krapovickas & Cristóbal 22414* (MO). Between Laguna de las Banduras and Fortín Fé, *N.N. in 1879* (CORD). El Condor near Viedma, *Cabrera et al. 19561* (LP, P). Carmen de Patagones, *Haumann in 1912* (BA). Dep. San Antonio, *Piccinini 1291, 1415, 1485, 1833* (BAB); *Hicken 37* (SI). Estuary of Río Negro, *N.N. 86* (LE). CHUBUT: Colonia Sarmiento, *O'Donell 3485* (LIL); *Cabrera 45* (LP). Puerto Madryn, *Dusén 5323* (SI); *O'Donell 3255* (LIL); *Soriano 2713* (BAB). Colonia San Martín, *Gerling 31* (POM). Gobernador Costa, *Birabén 580* (LP). Camarones, sea shore, *Aurelius 25* (S). Peninsula Valdez, *Rovereto 31-1537* (POM). Escalante, *O'Donell 3551* (LIL); *Kreibohm 110* (LP). Bahía Camarones (Port Sta. Elena), *Anderson 24 in 1826* (BM). Valley of Laguna Blanca, *Koslowsky 201* (BM, K, SI, Z). Esquel, *Castellanos in 1945* (F, LIL); *Eyerdam et al. 24575* (G, K, UC); *Kühnemann 647* (RSA). Corcovado, *Illin 6872, 6876* (BAB), *94* (BR, CORD, HBG, SI); *Soriano 3028* (CTES). Lago Futalaufquen, *Correa 4153* (BAB, UC); *Constance et al. in 1967* (BAA, MO); *Hicken 4, 14* (SI). El Maitén, *Meyer 9705* (LIL). SANTA CRUZ: Vicinity of Lago Argentino, *Dusén 5787* (S, SI); *Sleumer 1238* (LIL, US); *Boelcke 12509* (BAA, BAB); *Eyerdam et al. 24274* (G, GH, K, MO, SI, UC); *Scolnik 368* (RSA); *Furlong 99a* (GH, US), *5322* (NY); *Koslowsky 72* (CORD). Tehuelches, *Donat 54* (BM, G, GH, HBG, K, LIL, MO, NY, S, SI, UC, Z). Lago San Martín, *Rohmeder in 1945* (GH, LIL). San Julián, *Blake 56A* (LIL). Río Coyle, *Dauber 84* (POM). Río Gallegos, *Brown 62* (NY). Puerto Deseado, *Ancibor & Vizinis 4405* (BAA, MO); *Boelcke 12145* (BAA, BAB); *Eyerdam et al. 23869* (G, GH, K, MO, SI, UC), *O'Donell 3630* (LIL); *Anderson 49 in 1826* (POM). CÓRDOBA: Achiras, *Trelles* (SI-4853). LA PAMPA: Cerro Lihuel Calel, 400 m, *Burkart 20555* (P, SI); *Schwabe & Fabris 2028* (LP); *Krapovickas 3620* (BAB), *Krapovickas & Cristóbal 22384* (MO); *Troncoso in 1959* (SI); *Boelcke & Nicora 8120* (BAA, MO). General Acha, *Monticelli 10* (SI); *Troncoso in 1959* (SI). BUENOS AIRES: Balcarce, *Hunziker 3828* (POM). San Clemente near General Lavalle, *Cabrera 4921* (GH). Sierra La Tinta, *Spegazzini 40* (BAB). Quilmes, *Hicken in 1904* (SI). Mirimar, *Cabrera 5559* (LP). Mar del Sur, *Burkart 17876* (SI); *Nicora 17876* (SI, US). Pehuén-Có, *Correa 2299* (BAB); *Cabrera 14911* (LP, M); *Erettowi 2732* (MO); *Boelcke 11964* (SI). Bahía Blanca, *Ameghino 31-1628* (POM); *Job 1599* (NY). Bahía San Blas, *Fabris & Schwabe 5016* (CTES, M). Sierra Curamalal, *Spegazzini 18* (BAB); *Hohnberg in 1884* (CORD); *Burkart 4796* (BAA, CTES, MO); *Cabrera 5496* (LP); *Parodi 10355* (BAA, POM). Monte Hermoso, *Alboff in 1916* (LP); *Fabris & Schwabe 4817* (M); *Cabrera et al. 17055* (LP); *De Barba 633* (LIL); *Eskuche & Klein in 1968* (CTES). Quequén, *Castellanos 16092* (LIL); *Dawson 662* (LP, NY); *Rodriguez 828* (GH, LIL, NY). Necochea, *Nicora in 1961* (BAA), *7047* (MO); *Fabris & Schwabe 4759* (CTES, M, RSA); *Rodríguez 848* (GH, NY); *Eyerdam et al. 23709* (G, GH, K, UC). Sierra de la Ventana, *Alboff 124, 343* (CORD); *Cano & Cámara 227* (BAA, BAB); *Dawson 131* (LP), *Krapovickas 2958* (LIL, MO, RSA, SI); *Pastore 1205* (F, LIL, SI); *Abbiatti 4253* (NY). Olavarría, *Cabrera 20929* (P). Sierras del Azul, *Osten 152* (BREM).

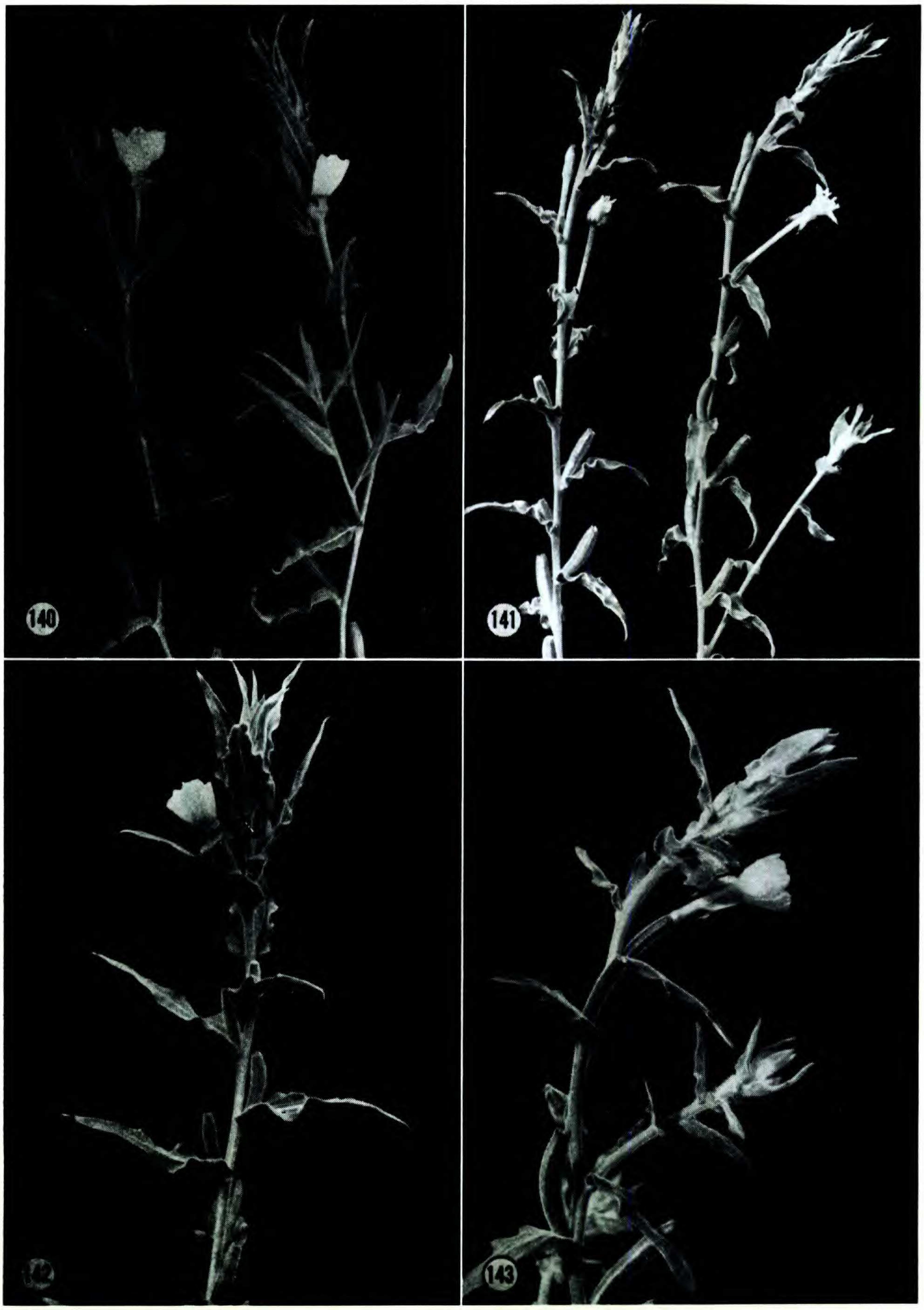
CHILE. AISÉN: Coihaique, *Rentzell 6129* pro parte (G, SI). Mina Silva near Lago Buenos Aires, *Heim in 1939* (Z). MAGELLANES: Puerto Prat, *Hicken 106* (SI).

Specimens from plants cultivated in gardens:

Hort. Kew, seeds from Port Desire, Argentina, *in 1791* (BM). Botanical Garden Paris, *in 1814*, Herb. *Cambessedes* (MPU). Botanical Garden Munich, Germany, *in 1814*, Herb. *Martius* (BR). Botanical Garden Arlary, *in 1827* (GH). Botanical Garden Munich, *in 1832* (M; as *O. undulata* Horti). Munich, *in 1833*, (BR; as *O. undulata*). Warsaw, Poland, *in 1834* (LE; as *O. undulata*). Botanical Garden Paris, *in 1842* (BR). Leningrad, USSR, *in 1847* (LE; as *O. dubia* F.M.). Leningrad, *in 1848* (LE; as *O. cognata*). Botanical Garden of Vienna, seeds from Berlin, *in 1856* (W; as *O. villosa*). Cultivated at Nymans, Sussex, England, 1929, *Comber 388* (K). Cultivated in Botanical Garden, Leningrad, seeds from *D. Nolte*, 1847 (LE; as *O. dubia* F.M.). Cultivated in Botanical Garden, Leningrad, 1847 (LE; as *O. cognata*).

Oenothera odorata reported in the literature from outside of South America:

GERMANY: Hegi (1925; pt. 2: 864).



FIGURES 140–143. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—140. *O. picensis* subsp. *picensis* (Argentina, Mendoza, *Santarius 1554*).—141. *O. picensis* subsp. *cordobensis* (Argentina, Jujuy, *Santarius 1845*).—142. *O. picensis* subsp. *bonariensis* (Argentina, Buenos Aires, *Santarius 370*).—143. *O. montevidensis* (Uruguay, Montevideo, *Santarius 1*).

Oenothera odorata is characterized by its large flowers with a relatively short floral tube; long, narrow fruits; and bracts broadly rounded at the base. Aside from *O. magellanica*, it is the only frequent member of the subsection in southernmost South America. This species is extraordinarily variable, but it is impossible to arrange its variability into an inclusive and useful taxonomic system; consequently, no infraspecific taxa are recognized. Especially pronounced is the variability in habit, hue of the stems and leaves, leaf shape, and pubescence.

Plants with plane leaves grow intermixed with others with somewhat undulate leaves in the same populations, in which intermediates also occur. Reddish or greenish coloration of the above-ground parts segregates in a Mendelian fashion, as it does in other species of the genus.

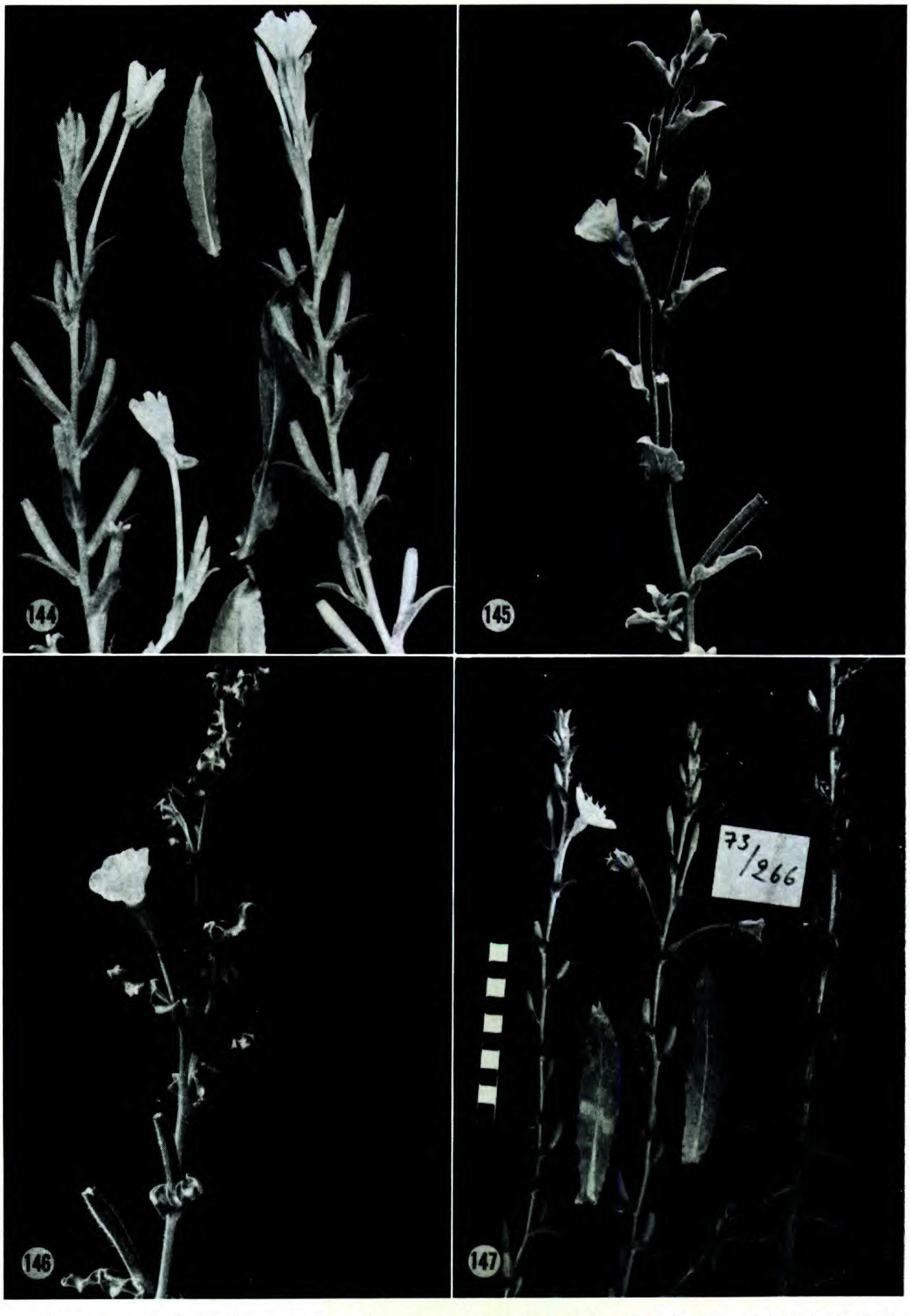
Plants with strigillose pubescence are completely absent in the northeast part of the range, in the province of Buenos Aires, but are widespread elsewhere. They predominate in the south, whereas populations consisting exclusively of plants with villous pubescence are more frequent in the north. Populations of this species in the province of Buenos Aires consist mainly of plants with an almost woolly pubescence, and are distinctive in this respect. Such populations have not been accorded taxonomic recognition, however, because they include, in addition to those with woolly pubescence, others which are identical to the less densely pubescent forms that are frequent in the provinces of La Pampa, Neuquén, and Río Negro.

The hairs that make up the so-called strigillose pubescence of *O. odorata* are not typical of those normally included in this category of pubescence in the species of series *Renneria*. In this series strigillose hairs are ca. 0.2 mm long and appressed closely to the stem, whereas in *O. odorata* they are about twice as long and generally erect, with only the tip curved toward the stem. The pubescence in *O. odorata* could therefore with justification be regarded as intermediate between strigillose and villous in character.

Oenothera odorata is extremely variable in its chromosomal configurations. Plants with 7 bivalents and all configurations up to and including complex heterozygotes with a ring of 14 occur. In the vicinity of Comodoro Rivadavia, Chubut Prov., the essentially stable configuration ring of 12 + 1 bivalent seems to have become predominant. This situation has been discussed further on p. 437.

16. **Oenothera ravenii** Dietrich, sp. nov.—FIGS. 6, 41–43, 47–49, 124–127, 176, 212.

Herba annua vel biennis, erecta, rosulata, simplex vel caulis principalis ramosus et ramis plerumque late arcuate vel rariore oblique e rosula ascendentibus, 5–10 dm alta. Plantae dense villosae, praecipue inferiore, sparseque glanduloso-pubescentes vel parce ad sparse strigulosi praecipue inferiore. Folia rosulae cultrata vel anguste oblanceolata, plerumque breviter acuta, basi acuta vel truncata, sessilia, 8–20 cm longa, 1.5–3 cm lata; folia caulina cultrata ad anguste oblonga vel lanceolata, acuta, basi truncata vel subcordata, sessilia, 3–15 cm longa, 0.8–1.5(–2) cm lata; bractea anguste ovata vel ovata, acuta, basi truncata vel subcordata, sessilia, plerumque quam capsulam subtena multo breviora, raro ad eam subaequalia, 1.5–3 cm longa, 0.5–1.5 cm lata; folia subintegria vel irregulariter obtuseque serrata, saepe marginibus praecipue in bracteis rubrescentibus. Inflorescentia simplex vel ramosa. Tubus floralis (2–) 3–5.5(–6.5) cm longus. Gemmae ambito oblongae vel lanceolatae, 1–3.5 cm longae, 5–11 mm



FIGURES 144–147. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—144. *O. pseudolongiflora* (Argentina, Buenos Aires, *Santarius 271*).—145. *O. parodiana* subsp. *parodiana* (Uruguay, Florida, *Santarius 211*).—146. *O. parodiana* subsp. *parodiana* (Argentina, Buenos Aires, *Santarius 468*).—147. *O. parodiana* subsp. ***brasiliensis*** (Argentina, Entre Ríos, ***Burkart*** *23423*).

crassae, plerumque junctura sepalorum tubo florali rubro-fasciatae, flavae vel flavido-virescentae, saepe rubrae. Sepala saepe dense vel sparse rubro-maculata; apices sepalorum erecti vel divergentes, 1–3 mm longi. Petala latissime obovata, lutea, saepe basi rubro-maculata, 1.2–5 (–5.5) cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato, vel brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.5–2.5 cm longum. Capsula 2.5–3.5 cm longa, 3–4 mm crassa, plerumque ab caulo directo subperpendicularo curvatum. Semina ambito elliptica vel rotundata, fusca, 1–1.5 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica, heterozygotica complexa, vel intermedia.

Erect annual or biennial herb, forming a rosette, unbranched or with a branched main stem and side branches which are usually widely arcuate but sometimes obliquely ascending from the rosette, 5–10 dm tall. Plants ± densely villous, especially below, and sparsely glandular-pubescent or moderately to sparsely strigillose, especially below. Rosette leaves cultrate to narrowly oblanceolate, mostly short acute, acute to truncate at the base, sessile, 8–20 cm long, 1.5–3 cm wide; cauline leaves cultrate to narrowly oblong or lanceolate, acute, truncate to subcordate at the base, sessile, 3–15 cm long, 0.8–1.5(–2) cm wide; bracts narrowly ovate to ovate, acute, truncate to subcordate at the base, sessile, mostly much shorter than the capsule they subtend, rarely ± the same length, 1.5–3 cm long, 0.5–1.5 cm wide; leaves plane or undulate at the margins, subentire or irregularly serrate with blunt teeth, often reddish along the margins, especially the bracts. Inflorescence branched or unbranched. Floral tube (2–)3–5.5(–6.5) cm long. Buds oblong to lanceolate in outline, 1–3.5 cm long, 5–11 mm thick, usually reddish at the junction of the sepals with the floral tube, yellow or yellowish green, often flushed with red. Sepals often densely or sparsely flecked with red; apices of the sepals erect or divergent, 1–3 mm long. Petals very broadly obovate, yellow, often with a red spot at the base, 1.2–5 (–5.5) cm long. Anthers 6–13 mm long. Filaments 8–27 mm long. Style long, the stigma held above the anthers at anthesis, or short, the anthers shedding pollen directly on the stigma at anthesis, 3–9 cm long. Stigma lobes 4–9 mm long. Ovary 1.5–2.5 cm long. Capsule 2.5–3.5 cm long, 3–4 mm thick, mostly curved directly outward from the stem. Seeds elliptic to rotund in outline, brown, 1–1.5 mm long, 0.5–0.7 mm thick. Self-compatible; outcrossing in those plants, all chromosomal homozygotes, in which the stigma is held above the anthers at anthesis, and self-pollinating in the rest. Gametic chromosome number, $n = 7$ (7 bivalents, ring of 14 or intermediate configurations at meiotic metaphase I).

Type: Grown from seed and cultivated in the Botanical Garden of Düsseldorf, Germany, 15 Aug. 1972. Source: Brazil, State of Rio Grande do Sul, Pelotas, 1966, *E. J. Hackbart* (MO-2155712, holotype; CTES, DUSS, M, isotypes).

Distribution (Figs. 225–226, 228, 243): In Brazil from Rio Grande do Sul north to the state of São Paulo; in Uruguay in the provinces of Salto, Cerro Largo, Rocha, Lavalleja, and Montevideo; in Argentina in the provinces of Misiones, Corrientes, Entre Ríos, Santa Fé, Buenos Aires, and Córdoba; in central Paraguay; and in Chile from Valdívia to Valparaíso.

This new species is dedicated to Peter H. Raven (1936–). Among its characteristics are the short, red-margined bracts and the sessile, usually oblong rosette and cauline leaves. Within this species subsp. *ravenii* is chromosomally homozygous, whereas subsp. *argentinae* and subsp. *chilensis* are entirely chromosomally heterozygous, but deriving both of their complexes from *O. ravenii*. Hybrids of chromosomal heterozygotes with homozygotes within this species yield only two closely similar phenotypes, both easily assignable to *O. ravenii*, in the F_1 generation. Similarly, hybrids with other homozygous species show that all elements included here within *O. ravenii* agree closely genetically despite their chromosomal differences.

KEY TO THE SUBSPECIES

1. Petals 2.5–5 cm long; stigma usually elevated above the anthers at anthesis; buds 2–3.5 cm long .... 16a. subsp. *ravenii*
1'. Petals 1.2–3 cm long; stigma surrounded by the anthers at anthesis; buds 1–2 cm long.
  2. Buds lanceolate in outline, 1–1.7 cm long; petals 1.2–2 cm long; seeds 1–1.3 mm long .... 16b. subsp. *argentinae*
  2'. Buds oblong in outline, 1.5–2 cm long; petals 2–2.5 cm long; seeds 1.3–1.5 mm long .... 16c. subsp. *chilensis*

16a. **Oenothera ravenii** subsp. **ravenii**.—FIGS. 6, 41–43, 124–125, 176, 212.

O. mollissima L. var. *paraguayensis* Chod., Bull. Herb. Boissier 7(9, app. 1): 71. 1899. LECTOTYPE: Paraguay, margins of forests near Cordillera de Altos, July (1885–1895), *E. Hassler 338* (G, holotype; G, P, isotypes); Hassler, Bull. Soc. Bot. Genève, sér. 2, 5: 274. 1913.

O. mollissima sensu Chodat, Bull. Herb. Boissier 7(9, app. 1): 71. 1899.

O. longiflora sensu Munz, Physis 11: 285. 1933, pro parte; Amer. J. Bot. 22: 663. 1935, pro parte; Comun. Bot. Mus. Hist. Nat. Montevideo 1(10): 35. 1943, pro parte; Fl. Brasílica 9(41): 55. 1947.

O. parodiana sensu Munz, Amer. J. Bot. 22: 662. 1935, pro parte.

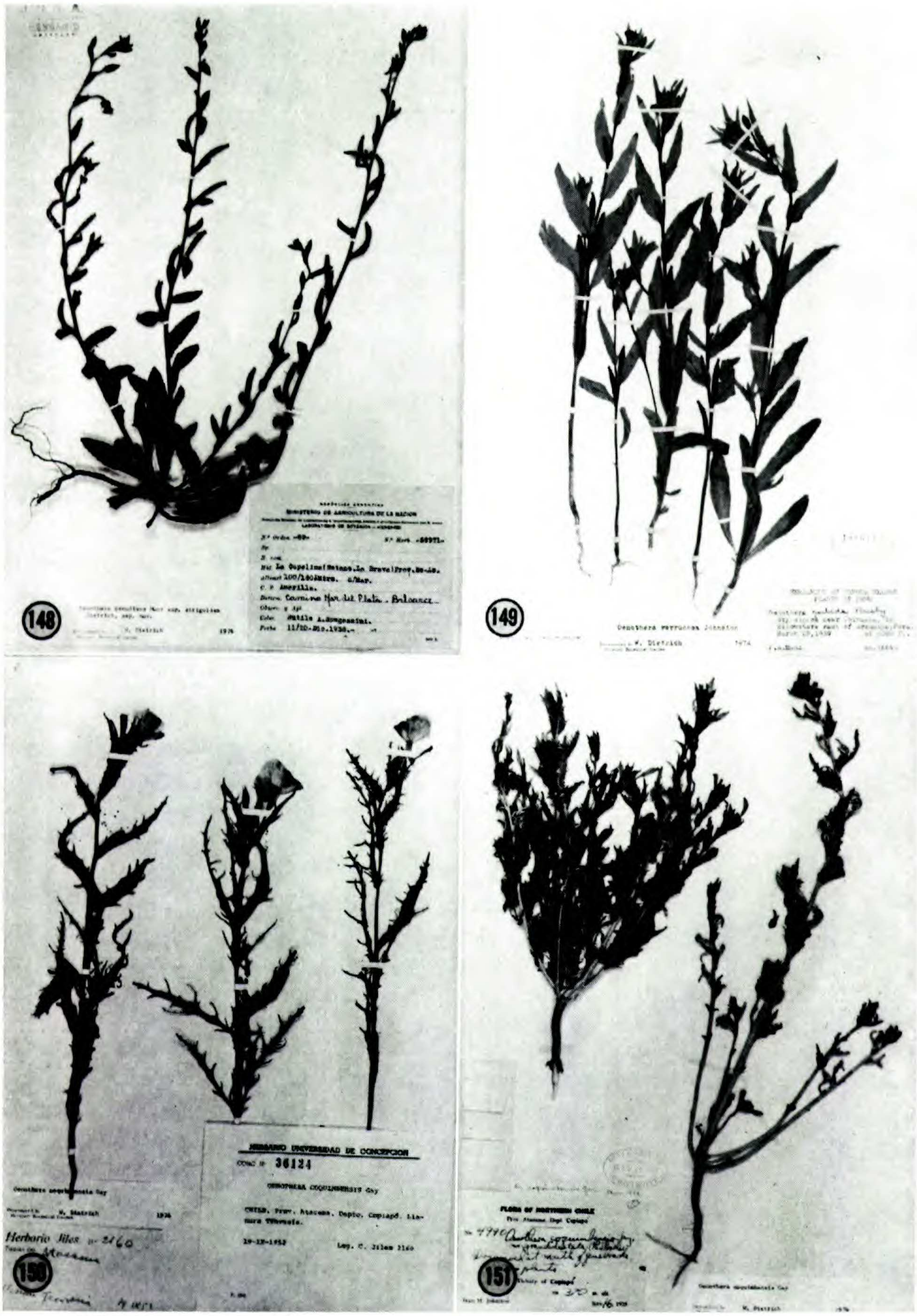
Rosette leaves cultrate to narrowly oblong or oblanceolate. Floral tube 3–5.5(–6.5) cm long. Buds lanceolate in outline, 2–3.5 cm long, 7–11 mm thick. Sepals reddish around the edges and often flecked with red on the surface; apices of the sepals 2–3 mm long. Petals 2.5–5 cm long. Anthers 8–13 mm long. Filaments 18–27 mm long. Style long, rarely short, the stigma usually elevated above the anthers at anthesis, 5.5–9 cm long. Stigma lobes 5–9 mm long. Ovary 1.5–2.5 cm long. Seeds 1.3–1.5 mm long, broadly elliptic in outline. Self-compatible but mostly outcrossing or self-pollinating and complex heterozygote. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 14** or small rings at meiotic metaphase I). Flowering time: October–June.

Distribution (Figs. 225, 243): Occurs in Brazil from Rio Grande do Sul north to Minas Gerais; in Uruguay in the provinces of Salto, Cerro Largo, Rocha, Lavalleja, and Montevideo; in central Paraguay; and in Argentina in the provinces of Misiones, Corrientes, Entre Ríos, and Santa Fé.

Specimens examined from cultivated plants:

BRAZIL. RIO GRANDE DO SUL: Pelotas, *Hackbart 1966** (ring of 6, 4 bivalents; ring of 8, ring of 4, 1 bivalent) (CTES, DUSS, M, MO). SANTA CATARINA: Coast near Ararangua, *Schultz in 1970* (ring of 4, 5 bivalents) (DUSS).

ARGENTINA. MISONES: At Ruta 12 near San Ignacio, *Conrad & Dietrich 26, 27* (ring of 6, 4 bivalents), *24* (2 rings of 6, 1 bivalent) (DUSS). CORRIENTES: Est. Garruchos near Santao Tomé, *Krapovickas 21464*** (DUSS).



FIGURES 148–151. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—148. *O. parodiana* subsp. *strigulosa* (Argentina, Buenos Aires, *Spegazzini in 1938*).—149. *O. verrucosa* (Peru, Arequipa, *Munz 15540*).—150. *O. coquimbensis* (Chile, Atacama, *Jiles 2160*).—151. *O. coquimbensis* (Chile, Atacama, *Johnston 4990*).

PARAGUAY. CORDILLERA: Roadside near Altos, ca. 10 km NE of San Bernardino, *Conrad & Dietrich 30***, *36*** (DUSS). Ca. 4 km SSE of San Bernardino, *Conrad & Dietrich 39*** (DUSS). CENTRAL: 3 km S of Aregua, *Conrad & Dietrich 50***, *53*** (DUSS).

Additional specimens examined:

BRAZIL. MINAS GERAIS: High fields in the Serra do Pieú, 1,800 m, *Schwacke 5248* (BR). SÃO PAULO: *St.-Hilaire 1498* (P). PARANÁ: Eng. Bley near Lapa, *Hatschbach 1067* (S, US). Between Jaguariaiva and Senges, *Hatschbach 9064* (HB, L). Roca Nova near Piraquara, *Hatschbach 1898* (RSA). Ponta Grossa, *Schwacke in 1874* (R); *Hoehne 23248* (SP). Curitiba, *Galvão in 1884* (R); *Stellfeld 1112* (SP). 50 km W of Guarapuava, 1,000 m, *Reitz & Klein 17713* (US). Agua Sta. Clara near Guarapuava, *Pereira 7967* (HB). Porto Amazonas, *Gurgel in 1929* (BR); *Gimpel 16163* (BR). Vila Velha, *Pereira & Pabst 7547* (M); *Dusén in 1904* (S); *N.N. in 1904* (R); *Hertel 52325* (SP); *Pereira 8272* (BR, HB). *Santa Catarina*: Bom Retiro, 1,650 m, *Smith & Klein 10435* (HBR, RSA, US). Ponte Alta near Curitibanos, 800–900 m, *Smith & Klein 8246* (HBR, NY, R, RSA, US). Agua Doce near Rio Chapeco, 12 km S of Horizonte, *Smith & Klein 13550* (HBR, RSA). Fazenda de Laranja, S. Joaquim near Bom Jardim, 1,400 m, *Reitz & Klein 7735, 7977* (HBR). Palhoca near Maciambu, *Reitz & Klein 980* (HBR). Garopaba, *Klein & Bresolin 8855* (HBR). Palmas near Joaçaba, 52 km W of Caçador, 1,000–1,300 m, *Smith & Reitz 9153* (US). Cangicas near Araranguá, 50 m, *Reitz C254* (BR, HBR). Sombrio near Araranguá, 10 m, *Reitz C1308* (GH, HBR). Campos Novos, 1,000 m, *Klein 4187* (HBR, RSA). RIO GRANDE DO SUL: Montenegro, *Henz 32563* (LIL). Uruguaiana, *Palacios & Cuezzo 210* (LIL). Between Cacapava do Sul and Morro Perao, *Palacios & Cuezzo 1449* (LIL). Between Alegrete and Capivari, *Palacios & Cuezzo 1919* (LIL). Itapoan, *Rambo 44448* (LIL). Near Farroupilha, *Rambo 42543* (LIL). Cerro de San Martinho near Sta. Maria, *Vidal 1508* (R). Rio Pardo, *Vidal 01570* (R). Between Capão de Canôa and Osório, *Nelson in 1970* (BR). Caaró near São Luiz, *Rambo 53349* (B). Lagoa Vermelha, *Rosengurtt 9078* (MVFA). Est. do Jaran near Quarai, *Rambo 26320* (LIL). Passo do Socorro near Vacaria, *Rambo 51383* (HBR). Pelotas, *Beetle 2236* (US); *Costa Sacco 690* (F, HB, R). Piratiny near Pelotas, *Malme 159* (S). S. Leopoldo, *Rambo 293* (LIL). Porto Alegre, *Molfino in 1898* (POM); *S. Barbara in 1835* (BR); *Rambo 27040* (LIL). Gloria near Porto Alegre, *Bornmüller 47* (GH); *Rambo 6461* (SP).

URUGUAY. CERRO LARGO: Río Branco, *Herter 2104* (F, MO, NY, US, Z). Bañado de los Burros, *Flossdorf 1* (POM, SI). Arroyo Zapallar, *Praderi 742* (LIL). SALTO: Thermal Springs of Arapey, *Rosengurtt 10569* (MVFA). Paso del Arroyo Las Cañas, *Rosengurtt B1058* (POM). ROCHA: Castillos, *Herter 987938* (POM). E coast of Uruguay, *St.-Hilaire 2213* (P). LAVALLEJA: Road to Puma near Minas, *Osten 4490* (G). C. Verdún near Minas, *Berro 6246* (MVFA). MONTEVIDEO: Punta Gorda, *Osten 22088* (GH).

ARGENTINA. MISIONES: Candelaria, *Bertoni 2463* (LIL); *Descole 3270* (LIL); *Sesmero 83* (LIL). Loreto near Candelaria, 290 m, *Montes 58B* (US). At Ruta 14 near Arroyo Garupá Norte, *Krapovickas et al.* (CTES). Garupá near Candelaria, *Bertoni 4734* (LIL). Pindapoy near Candelaria, *Bertoni 3862* (LIL). Santa Ana, *Bertoni in 1944* (LIL); *Sesmero 168* (LIL, NY); *Rodríguez 671* (BA, LIL, POM, SI, UC); *Schwarz 632* (LIL, NY, UC); *Montes 1516* (RSA); *Rodríguez 158* (LIL). San José, *Sesmero 241* (LIL). Posadas, *Gallando 3739* (SI); *Bertoni 1514* (LIL). Mártires near Posadas, 130 m, *Bertoni 5724* (LIL). Posadas, *Ekman 2029* (G, LD, S, US). Cerro Corá, *Crovetto 9492* (BAB). Puerto Leoni near Cainguas, *Schwarz 1575* (LIL). Apostoles, *Ibarrola 1051* (BR, LIL, NY). Santa Irene near San Javier, *Bertoni 526* (LIL). Corpus near Santa Ana, *Bertoni 1866* (LIL). Sto. Tomás, 160 m, *Bertoni 4696* (LIL). Santa Inés, *Meyer 11439* (LIL). Concepción, *Schwarz 3566* (LIL, RSA). Arroyo Jabebiri, *Meyer 11512* (LIL). Villa Samis, *N.N. in 1944* (LIL). El Dorado near Iguazú, *Schwartz 2042* (LIL). Puerto Wanda near Iguazú, *Montes 9591* (LIL). Puerto Istuela, *Montes 10117* (LP). Arroyo Apepú near San Ignacio, *Schwarz 2882* (LIL). Menóchio near San Ignacio, *Schwarz 1255* (LIL). San Ignacio, *Medina 212* (LIL, RSA). CORRIENTES: Estancia "Santa Teresa," *Pedersen 93* pro parte (S, US). Est. "Garruchos" near Santo Tomé, *Pedersen 9229* (C); *Krapovickas et al. 21464* (MO). At Ruta 14 near Gob. Virasoro, *Krapovickas et al. 16692, 16753* (CTES). Est. San Francisco, 23 km NW of Gob. Virasoro, *Krapovickas et al. 17217* (CTES). Paso Pucú near Concepción *Pedersen 7482* (C). Baibiene, *Castellanos 34445* (RSA). S. Roqueito near Mercedes, *Irigoyen 71* (CTES). San Carlos near Ituzaingó, *Krapovickas et al. 17995* (CTES). Yahápe at Ruta 12 near Berón de Astrada, *Krapovickas et al. 16537* (CTES). ENTRE RÍOS: Concepción del Uruguay, *Lorentz in 1876* (BM). SANTA FÉ: Road to Requoncista, *Job 974* (NY).

PARAGUAY. Cordillera de Altos, *Fiebrig 434* (F, G, GH, HBG, K, L, LY, M); *Hassler 338* (G, P), *744* (G, K, P). San Bernardino, *Hassler 3343* (BM, G, GH, K, LY, NY, P, W). Near

Igatimi, *Hassler 5567* (BM, G, GH, K, LIL, LY, MO, MPU, P, S, UC, W); *Töppen in 1883* (HBG). Vicinity of the river Y-aca, *Hassler 6879* (BM, G, GH, K, LIL, LY, MICH, MO, MPU, NY, P, S, UC, W). Vicinity of the lake Ypacaray, *Hassler 12486* (BM, C, F, G, GH, K, L, LIL, LY, MICH, MO, NY, S, UC, US, Z). Villa Elisa, *Pedersen 5125* (C). Caáguazú, *Balansa 2220* (G, P, RSA); *Hassler 8996* (BM, G, K, NY, W); *Töppen in 1883* (HBG). Tapytá, *Jörgensen 4754* (F, MO, NY, POM, S, SI, US). Sapucaí, *Götzsche in 1891* (CORD). Pirareta near Paraguarí, *Sparre & Vervoorst 173* (LIL). Chololo near Paraguarí, *Sparre & Vervoorst 613* (LIL). Encarnación, 110 m, *Bertoni 4524* (LIL); *Schrottky 116* (LIL).

Early specimens from plants cultivated in Botanical Gardens:

Rovig in 1818 (CORD; as *O. longiflora*). From the Garden of Mr. Ohm at Berlin, *Bauer in 1838* (CORD; as *O. sellowiana*). From Botanical Garden at Berlin, *Bauer in 1842* (CORD; as *O. sellowiana*).

Oenothera odorata and *O. featherstonei* are the only entities that regularly exceed *O. ravenii* subsp. *ravenii* in flower size. In this subspecies, plants with red-flecked and entirely green sepals grow intermixed in the same populations, and the characteristic seems to segregate in a Mendelian fashion. Plants from Brazil, Uruguay, and the provinces of Corrientes and Entre Ríos in Argentina are moderately pubescent, whereas those from the Province of Misiones in Argentina are very densely pubescent, especially in their lower portions.

On the map of distribution of the *ravenii*-complex (Fig. 243), it can be seen that this chromosomal complex exists in homozygous form only in the northeastern portion of the range. Evidently, this complex combines readily with others as discussed under species no. 23, 27, 28, 36, 37 and 41. As the ancestors of *O. ravenii* migrated east from a probable area of origin in the vicinity of Tucumán, they seem to have hybridized readily with others, and the homozygotes persist today only at the very margins of the range.

Just as in *O. odorata*, the existence of an array of chromosomally differentiated homozygotes may be inferred within this entity, the hybridization of which has given rise to the complex heterozygotes. In Düsseldorf two chromosomally homozygous plants (*72-1227a* and *72-1228*) from the same locality near Pelotas were crossed and gave rise in the F_1 generation to a plant (*73-576*) with a ring of 14 chromosomes, showing that such potentiality existed also within the original population.

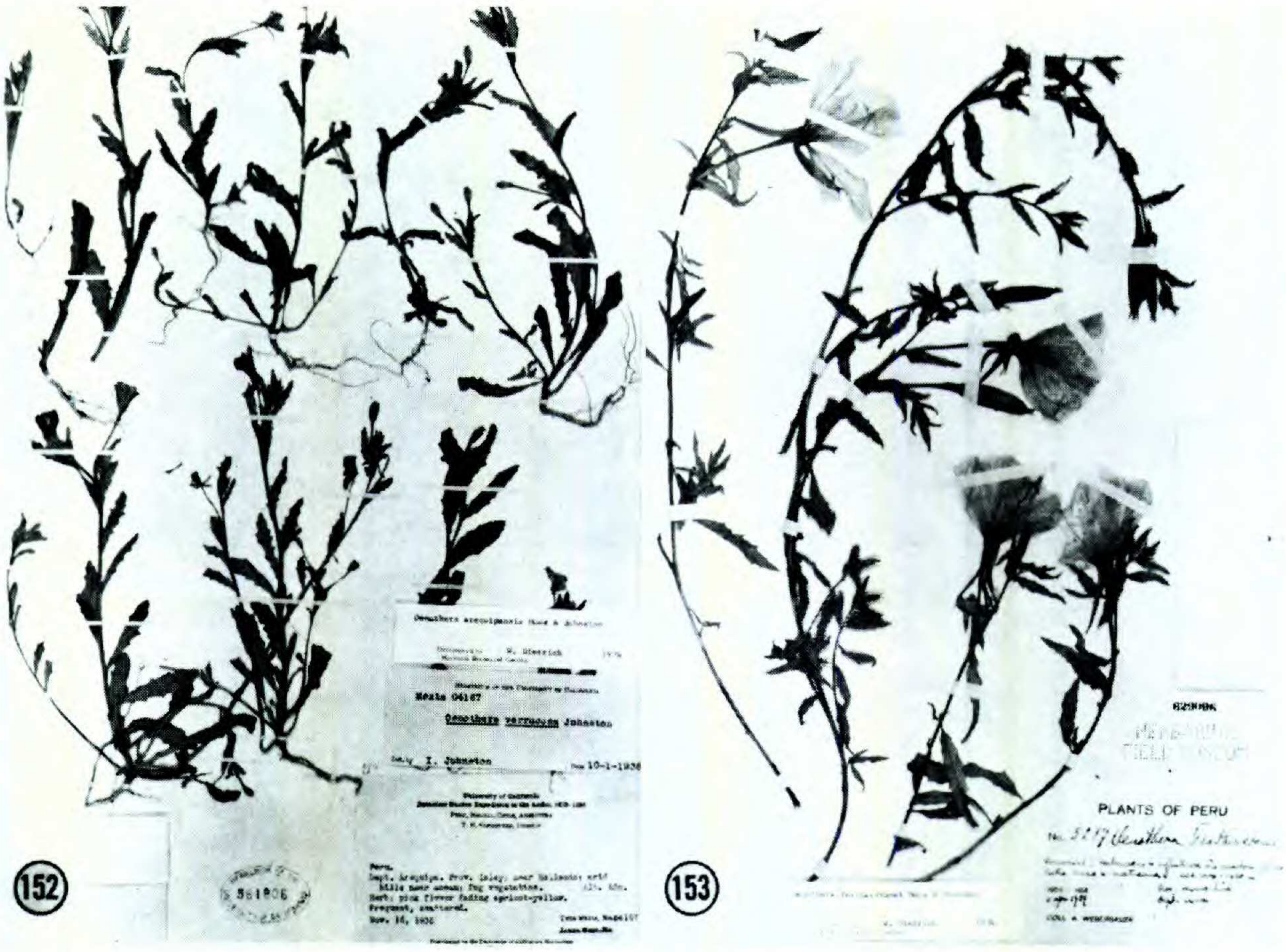
16b. **Oenothera ravenii** subsp. **argentinae** Dietrich, subsp. nov.—Fig. 126.

O. parodiana sensu Munz, Physis 11: 283. 1933, pro parte; Amer. J. Bot. 22: 662. 1935, pro parte.

O. stricta sensu Munz, Physis 11: 285. 1933, pro parte.

Folia ut in subsp. *ravenii*. Tubus floralis 1.8–3.5 cm longus. Gemmae ambito lanceolatae, 1–1.7 cm longae, 5–7 mm crassae. Sepala rubro-marginata, saepe etiam rubro-maculata; apices sepalorum 1–2 mm longi. Petala 1.2–2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.3–1.5 cm longum. Semina 1–1.3 mm longa, 0.5–0.7 mm crassa, ambito rotundata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Leaves as in subsp. *ravenii*. Floral tube 1.8–3.5 cm long. Buds lanceolate in outline, 1–1.7 cm long, 5–7 mm thick. Sepals with red margins, often also flecked with red; apices of the sepals 1–2 mm long. Petals 1.2–2 cm long. Anthers 6–8 mm long. Filaments 12–15 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 3–4.5 cm long. Stigma lobes 4–5 mm



FIGURES 152–153. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—152. *O. arequipensis* (Peru, Arequipa, *Mexia 04167*).—153. *O. featherstonei* (Peru, Lima, *Weberbauer 5217*).

long. Ovary 1.3–1.5 cm long. Seeds 1–1.3 mm long, 0.5–0.7 mm thick, rotund in outline. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 12 and 1 bivalent** at meiotic metaphase I). Flowering time: October–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Córdoba, Copina near Córdoba, Dec. 1961, *G. Göpel* (MO-2155709, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 228): In Brazil, so far known only from the state of Rio Grande; the southern departments of Canelones, Maldonado, and Florida in Uruguay; and the provinces of Entre Ríos, Buenos Aires, and Córdoba in Argentina.

Specimens examined from cultivated plants:

BRAZIL. RIO GRANDE DO SUL: Pelotas, *Hackbart in 1966** (DUSS, M); *Hackbart in 1967**,** (DUSS).

ARGENTINA. ENTRE RÍOS: Concepción del Uruguay, *Burkart in 1961** (DUSS). CÓRDOBA: Copina near Córdoba, *Göpel in 1961** (DUSS, M, MO). BUENOS AIRES: Mar de la Plata, *Santarius 342** (CTES, DUSS, MO).

URUGUAY. FLORIDA: Florida, *Hecht 1964-31** (DUSS). Mansavillagra, *Santarius 231** (CTES, DUSS, MO).

Additional specimens examined:

BRAZIL. RIO GRANDE DO SUL: Near Caçapava, road to São Sepé, *Rosengurtt 8736* (MVFA).

URUGUAY. MONTEVIDEO: Montevideo, *Arillaga 721* (MVFA). FLORIDA: Casuja, *Borsani 5564* (MVFA). CANELONES: Arroyo Sarandi, *Izaguirre 154* (MVFA).

ARGENTINA. ENTRE RÍOS: Concepción del Uruguay, *Lorentz in 1876* (GH). BUENOS AIRES: Vicinity of Junín, *Saint-Ives 173* (G). Sierra de la Ventana, *N.N. 12789* (LP). Est. San Juan, 30 km S of Buenos Aires, *Eyerdam 23037a* (G, GH, K, MO, UC). 20 km N of Mar del Plata, road to Balcarce, *Eyerdam et al. 23644, 23669* (GH, K, UC). "La Brava" near Balcarce, *Lourteig 162* (LIL); *Capurro in 1941* (LIL). Cerro El Sombrerito near Tandil, 550 m, *Huidrobo 1770* (LIL, NY). El Dia, *King 263* (BM). Delta del Paraná, Río Cabo, *Burkart 5119* (BAA). CÓRDOBA: Sierra Grande, Copina, *Hunziker 11439* (CORD, MO). Sierra Achala, *Hieronymus 335* (P).

Oenothera ravenii subsp. *argentinae* is a complex heterozygote which can be distinguished from the chromosomally homozygous subsp. *ravenii* only by its smaller flowers. The plants of subsp. *argentinae* seem more vigorous in growth than those of subsp. *ravenii* and may eventually replace them. Populations of subsp. *argentinae* that occur within the area of subsp. *ravenii* have, as a rule, larger flowers than those which occur beyond this area, in the Province of Buenos Aires. Populations of subsp. *argentinae* probably represent an early phase in the stabilization of their complex heterozygosity.

16c. **Oenothera ravenii** subsp. **chilensis** Dietrich, subsp. nov.—FIGS. 47–49, 127.

Folia rosulae anguste oblanceolata vel oblanceolata. Tubus floralis 2–3.5 cm longus. Gemmae ambito oblongae, 1.5–2 cm longae, 5–6 mm crassae, junctura sepalorum tubo florali rubro-fasciatae. Sepala immaculata; apices sepalorum 1.5–2 mm longi. Petala 2–2.5 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.2–2 cm longum. Semina 1.3–1.5 mm longa, 0.5–0.6 mm crassa, ambito late elliptica. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Rosette leaves narrowly oblanceolate to oblanceolate. Floral tube 2–3.5 cm long. Buds oblong in outline, 1.5–2 cm long, 5–6 mm thick, red at the junction of the sepals with the floral tube. Sepals not red-flecked; apices of the sepals 1.5–2 mm long. Petals 2–2.5 cm long. Anthers 6–8 mm long. Filaments 8–13 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 3–5 cm long. Stigma lobes 4–7 mm long. Ovary 1.2–2 cm long. Seeds 1.3–1.5 mm long, 0.5–0.6 mm thick, broadly elliptic in outline. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–February.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 24 July 1973. Source: Chile, Prov. Cautín, Molco at Lago Villarica, 1960, *W. Stubbe* (MO-2155707, holotype; CTES, DUSS, M, MO, isotypes).

Distribution (Fig. 226): In Chile from the provinces of Valdívia to Valparaíso.

Specimens examined from cultivated plants:

CHILE. CAUTÍN: Fundo Doyín near Loncoche, *Stubbe in 1960** (CTES, DUSS, M, MO). Molco at Lago Villarica, *Koch in 1961* (DUSS); *Stubbe in 1960** (DUSS, M, MO).

Additional specimens examined:

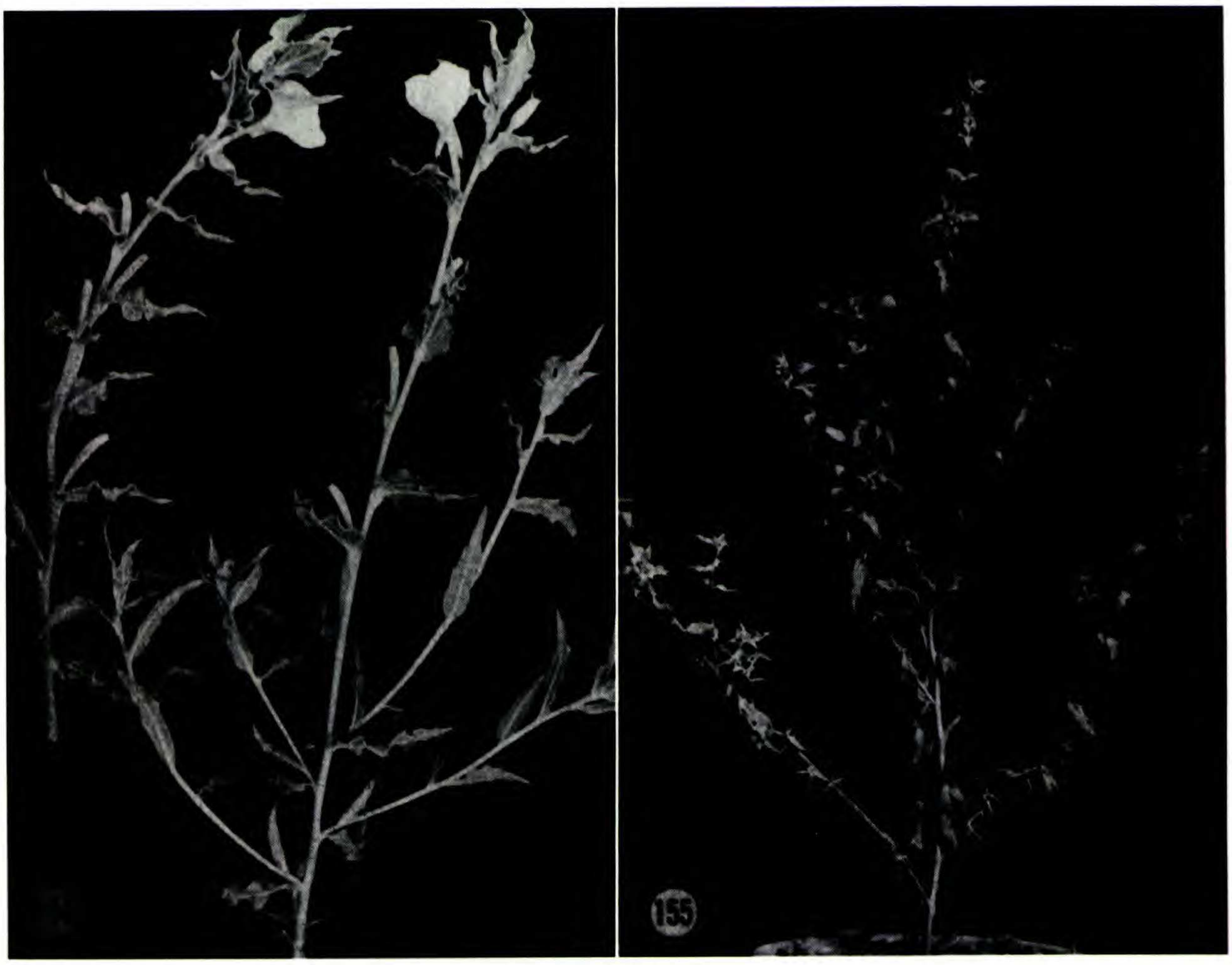
CHILE. VALPARAÍSO: Valparaíso, *Buchtien in 1895* (US). CONCEPCIÓN: At km 15 between Concepción and Coronel, *Cea & Ugarte in 1967* (CONC-35028). At km 42 between Concepción and Bulnes, *Villarroel & Weldt 119* (CONC). Near Concepción, *Macrae in 1825* (G, NY). MALLECO: Fundo San Elias near Victoria, 300 m, *Sparre 3315* (S). VALDIVIA: Panguipulli, 230 m, *Hollermayer 562* (M). Quinchilca, *Hollermayer 65a* (LP).

Oenothera ravenii subsp. *chilensis* can be distinguished from both other subspecies by its medium-sized flowers, buds oblong in outline, and consistently oblanceolate leaves. It apparently arose from Chilean populations of the complex heterozygote *O. stricta* subsp. *stricta* by the segregation of two genomes originally derived from subsp. *ravenii* and the reconstitution of a chromosomally homozygous series of populations west of the Andes. In cultivated plants the influence of *O. odorata* on *O. ravenii* subsp. *chilensis* can be seen, especially in the form of the rosette leaves. This influence has come about because of crossing-over between the *ravenii*-genome and the *odorata*-genome within the complex heterozygote *O. stricta* subsp. *stricta.* The genomes of *O. ravenii* that segregated from *O. stricta* subsp. *stricta* apparently were modified in this way, and the resulting populations, although primarily *O. ravenii,* show the influence of *O. odorata.* In a similar manner, *O. affinis* seems to have modified Paraguayan populations of *O. ravenii* subsp. *ravenii.*

17. **Oenothera longiflora** L., Mant. Pl. 227. 1771.—FIGS. 50–52, 55–57, 128–129, 177, 213–214.

Erect annual or biennial herb, forming a rosette, unbranched or with a branched main stem and widely arcuately ascending side branches arising from the rosette, 4–8 dm tall. Entire plant densely long-villous and sparsely glandular-pubescent. Rosette leaves narrowly elliptic to elliptic or oblanceolate to narrowly obovate, short-acute, gradually narrowed to a short petiole or sessile, cuneate at the base, 6–18 cm long, 1.5–3.5 cm wide; cauline leaves oblong to elliptic or narrowly ovate to ovate, short-acute, truncate to subcordate at the base, sessile, 1.5–6 cm long, 1–3 cm wide; bracts oblong to broadly oblong or ovate, short-acute or subobtuse, truncate to subcordate at the base, sessile, those of the central and upper portions of the inflorescence much shorter than the capsule they subtend, 1–3 cm long, 1–3 cm wide; leaves mostly irregularly serrate, the teeth blunt or acute, plane or undulate along the margins; bracts usually red along the margins. Inflorescence branched. Floral tube (6.5–)8–10 cm long, often streaked and flecked with dark red. Buds narrowly oblong to lanceolate in outline, red at the junction of the sepals with the floral tube, 2–3.5 cm long, 5–11 mm thick. Sepals green to yellowish green, often streaked and flecked with red; apices of the sepals erect or divergent, 1–3 mm long. Petals very broadly obovate, yellow, often with a red spot at the base, 2–4 cm long. Anthers 7–13 mm long. Filaments 14–24 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, or the style long, the stigma held above the anthers at anthesis, 8–13 cm long. Stigma lobes 6–12 mm long. Ovary 1.7–2 cm long. Capsule mostly curved and with 4 clearly distinct crenate valves at the apex, 3–4.5 cm long, 3–4 mm thick. Seeds elliptic to broadly elliptic, brown, 1.5–2 mm long, 0.8–1.1 mm thick. Self-compatible; self-pollinating and complex heterozygote. Gametic chromosome number, $n = 7$ (7 bivalents, ring of 14 or ring of 12 and 1 bivalent at meiotic metaphase I). Flowering time: October–March.

Type: Cultivated at Uppsala, Sweden, the seeds from the vicinity of Buenos Aires, Argentina, grown in 1752 or earlier, *C. Linnaeus* (LINN, holotype, POM photograph).



FIGURES 154–155. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—154. *O. grisea* (Chile, Valparaíso, Las Ventanas, *Constance in 1965*).—155. *O. nocturna* (Peru, Lima, *Santarius 2333*).

Distribution (Figs. 229–230): In Brazil only in Rio Grande do Sul; in Uruguay in the departments of Río Negro, Colonia, San José, and Montevideo; and in Argentina in the provinces of Corrientes, Entre Ríos, and Buenos Aires.

Oenothera longiflora is unmistakable because of its dense long-villous pubescence and long floral tube. It is characteristic of sandy places along rivers and near the coast. This species is related to *O. ravenii*, as shown by similarities in habit, short bracts, reddish leaf margins, and the red basal spot on each petal. The seeds of *O. longiflora* are the largest in the series.

Oenothera longiflora subsp. *grandiflora* is chromosomally homozygous, subsp. *longiflora* is chromosomally heterozygous. The latter has two complexes from subsp. *grandiflora*, but one of them appears to have been influenced by introgression from *O. ravenii*. Among the F_1 progeny derived from crossing the heterozygote *O. longiflora* subsp. *longiflora* with *O. ravenii*, there are two classes of progeny, one intermediate and the other more similar to *O. ravenii*. The influence of the "pure" *O. longiflora* subsp. *grandiflora* genome upon the characteristics of *O. longiflora* subsp. *longiflora* is so strong, however, that it seems undesirable to recognize this particular complex heterozygote as a species separate from subsp. *grandiflora*.

Oenothera longiflora subsp. *grandiflora* is evidently very rare and occurs only at scattered localities. It may either have a relictual distribution, therefore, or be derived as a viable homozygous segregate from the chromosomally structurally heterozygous subsp. *longiflora.*

KEY TO THE SUBSPECIES

1. Style long, the stigma held above the anthers at anthesis; buds 2.5–3.5 cm long; petals 3–4 cm long .... 17a. subsp. *grandiflora*
1'. Style short, the anthers shedding pollen directly on the stigma at anthesis; buds 2–2.5 cm long; petals 2–3 cm long .... 17b. subsp. *longiflora*

17a. **Oenothera longiflora** subsp. **grandiflora** Dietrich, subsp. nov.—FIGS. 50–52, 128, 177, 213.

Folia rosulae 2.5–3.5 cm lata; folia caulina 2–3 cm lata; bractea 1.5–2 cm lata, 1.5–2.5 cm longa. Gemmae 2.5–3.5 cm longae, 8–11 mm crassae; apices sepalorum divergentes, ca. 3 mm longi. Petala 3–4 cm longa, basi rubro-maculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Rosette leaves 2.5–3.5 cm wide; cauline leaves 2–3 cm wide; bracts 1.5–2 cm wide, 1.5–2.5 cm long. Buds 2.5–3.5 cm long, 8–11 mm thick; apices of the sepals divergent, ca. 3 mm long. Petals 3–4 cm long, with a red spot at the base of each one. Anthers 10–13 mm long. Filaments 22–24 mm long. Stigma lobes 8–12 mm long. Style long, the stigma elevated above the anthers at anthesis. Self-compatible. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 19 Oct. 1972. Source: Argentina, Prov. Corrientes, Paso de los Libres, 27 Mar. 1964, *A. Krapovickas & C. Cristóbal 11293* (MO-2155211, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 229): Known only from the type locality and one locality in the province of Entre Ríos, Argentina.

Specimen examined from cultivated plants:

ARGENTINA. CORRIENTES: Paso de los Libres, *Krapovickas & Cristóbal 11293* (DUSS, M, MO).

Additional specimens examined:

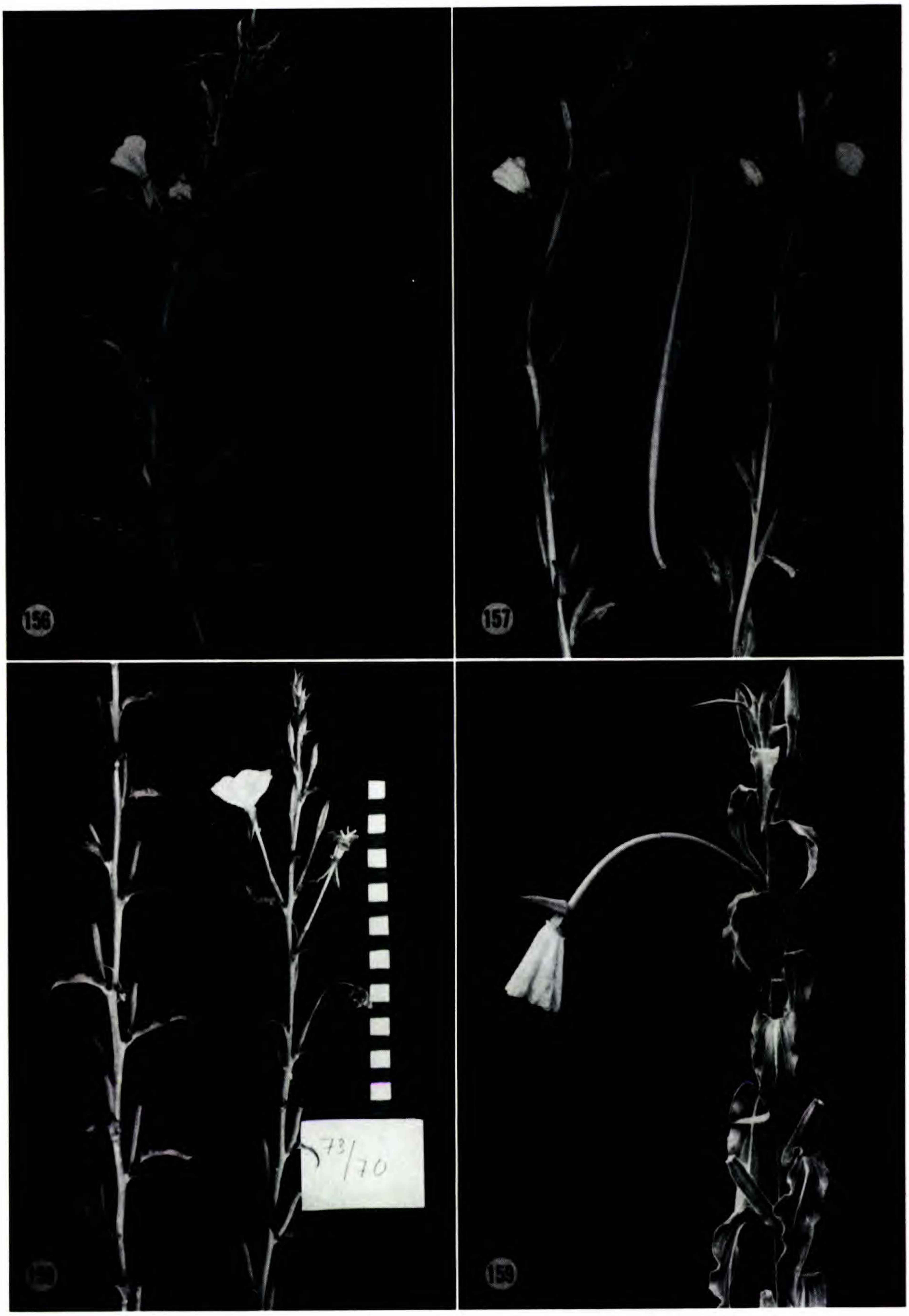
ARGENTINA. ENTRE RÍOS: Dep Federación, Santa Ana at Río Uruguay, *Burkart 29273, 26317* (SI).

In 1962 and 1963 there appeared in Düsseldorf among the progeny of plants growing wild in the Botanical Garden of Buenos Aires (*Göpel in 1961*), one plant with 7 bivalents and another with a ring of 4 and 5 bivalents. Unfortunately, both of these strains were lost, since a test-progeny grown in 1973 yielded only plants with a ring of 12 and 1 bivalent which would therefore be referred to *O. longiflora* subsp. *longiflora.*

17b. **Oenothera longiflora** subsp. **longiflora**.—FIGS. 55–57, 129, 214.

Onagra pellucida Moench, Meth. Pl. 1: 675. 1794. TYPE: The herbarium of Moench apparently no longer exists.

Onothera polymorpha H. Lév. race *longiflora* (L.) H. Lév., Mongr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 324. 1909.



FIGURES 156–159. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—156. *O. magellanica* (Argentina, Mendoza, *Santarius 1581*).—157. *O. villaricae* (Chile, Cautín, *Göpel in 1961*).—158. *O. hechtii* (Argentina, Tucumán, *Hecht 1964-81*).—159. *O. elongata* (Bolivia, Tarija, *Santarius 1956*).

O. polymorpha race *longiflora* var. *sellowii* Link & Otto ex H. Lév., Monogr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 324. 1909. LECTOTYPE: Cape Verde Islands, Brava, mountains, 900 m, 30 Mar. 1864, *R. T. Lowe* (BM; P, isolectotype). Locality given in error as being in Bolivia by H. Léveillé.

Oenothera mollissima L. var. *longiflora* (L.) Hassler, Bull. Soc. Bot. Genève, sér. 2, 5: 274. 1913.

Raimannia longiflora (L.) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.

Rosette leaves 1.5–2.5 cm wide; cauline leaves 1.5–2.5 cm wide; bracts 1–1.5 cm long, 1–1.5 cm wide. Buds 2–2.5 cm long; apices of the sepals erect, 1–2 mm long. Petals 2–3 cm long, often with a red spot at the base of each one. Anthers 7–12 mm long. Filaments 14–22 mm long. Stigma lobes 6–8 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 12 and 1 bivalent** at meiotic metaphase I).

Distribution (Fig. 230): In Brazil only in Rio Grande do Sul; in Uruguay in the departments of Río Negro, Colonia, San José, and Montevideo; and in Argentina in the provinces of Entre Ríos and Buenos Aires. Not known from the province of Corrientes in Argentina, where *O. longiflora* subsp. *grandiflora* occurs.

Specimens examined from cultivated plants:

URUGUAY. COLONIA: Sandy places at the northern entrance of Juan L. Lacaze, *Santarius 73*, 74*, 77, 79, 80, 81*, 82–84, 86,* 87, 88,* 89, 90* (DUSS; 81 also CTES; 73, 81 also M; 73, 81, 89 also MO). Dunes NW of Juan L. Lacaze, *Santarius 109–115, 116** (DUSS; *116* also M; *109, 116* also MO).

ARGENTINA. BUENOS AIRES: Wild in the Botanical Garden of Buenos Aires, *Göpel in 1961*** (DUSS, M). La Plata, *Hecht 1964-22** (CTES, DUSS, M). Villa Ortuzor in Buenos Aires, *Hecht 1964-123* (DUSS, M).

Additional specimens examined:

BRAZIL. RIO GRANDE DO SUL: Rio Grande, *Gaudichaud 1287* (P).

URUGUAY. RÍO NEGRO: San Javier, *Puerto 8415* (MVFA); *Herter 82853* (POM). COLONIA: Colonia, *Molfino 31-1650* (POM); *N.N. 27* (BAA). Dunes near Riachuelo, *Cabrera 3856, 3345* (LP). SAN JOSÉ: Arazati, *Arrillaga 641* (MVFA). Playa Pascual, *Arrillaga 741* (MVFA). MONTEVIDEO: Montevideo, *Fruchard in 1874* (RSA); *Barattini in 1939* (MO); *N.N.* (MPU); *Lorentz 307* (G). Sta. Lucía, *Fruchard in 1874* (US); *Fruchard in 1875* (P). Coast near Montevideo, *Gibert 339* (K). Maluni, *Rosa-Mato 1525* (LIL). Punta Gorda, *Osten 4664* (G), *22709a* (GH). Between La Colorada and Pajas Blancas, *Lema 6458* (F, MVFA). Miguelete, *Berro 5340* (MVFA). Cerro, *Herter 162* (F, G, GH, HBG, LE, M, MO, POM, S, Z). Buceo, *Felippone 2895, 5971* (SI). Carrasco, *Fruchard in 1875* (P); *Osten 5784* (CORD, US); *Felippone 6097* (SI); *Legrand 343* (POM); *Rosengurtt B418* (POM). Malvín, *Felippone 3342* (SI). ROCHA: Eastern coast, *Tweedie 78* (BM).

ARGENTINA. BUENOS AIRES: Dock Sur, *Hicken 784* (LIL, SI); *Molfino 221* (POM). Pellegrini, *Cabrera 6954* (LP, NY). Devoto, *Hirschborn 40* (POM). Maciel, *Molfino 25842* (SP). La Plata, *Hirschborn 676* (POM). Paternal, *Parodi 8993* (GH, K, POM). Carón, *Franqueville* (P). ENTRE RÍOS: Concepción del Uruguay, *Lorentz 1230* (CORD, G, SI). Concordia, *Spegazzini 88* (BAB). Santa Ana, *Gamerro 1310* (LP). Berduc, *Crovetto & Piccinini 4654* (BAB). El Palmar, *Pedelaborde in 1940* (SI). Between Gómez and Emb. Ferrari near Concordia, *Meyer 10974* (LIL).

Specimens from outside of South America (naturalized):

FRANCE. Near Bayonne, *Lange in 1851* (P); *Bordère in 1877* (G); *Blanchet in 1880* (P). Between Bayonne and Boucau, 1881, *Blanchet 70* (LISU, LY, MPU, P); *Neyraut in 1889* (COI, MPU); 1933, *Hibon 1461-2* (P). Boucau, *Deflers in 1879* (MPU); *Neyraut in 1902* (LY); *Willkomm* (COI). Dep. Landes, Rivière, *Foucaud in 1881, in 1882* (LY). Biarritz, *Henry in 1903* (B). Anglet, *Neyraut in 1905* (MPU).

PORTUGAL. Açores, Fayal, *Donat in 1868* (G, P). MADEIRA: Serro de S. Roque, 1865–

1866, *Mandon 441* (G, P). Mountains above the Povoação, *N.N. 766, 768* (K); *Lowe in 1866* (BM).

SPAIN. CANARY ISLANDS: Puerto de La Orotava, *N.N. 2352* (K).

SOUTH AFRICA. CAPE: Camps Bay, *BS. in 1846* (K); *Prior in 1846* (PRE). Wellington, *Thomson in 1881* (PRE). Cape of Good Hope, *Pappe* (K).

AUSTRALIA. NEW SOUTH WALES: Raymond Terrace, *Coans in 1961* (NSW-65372). Princess Highway at crossing of Minimurra River, 1 mi S of Albion Park, *Raven et al. 25895 in 1970* (MO, NSW); *Briggs 3950 in 1970* (NSW).

Hybrids with *O. stricta* subsp. *stricta* have been collected in France, where both species grow together near Biarritz: Biarritz, *Cornuault in 1907* (MPU). Anglet, 1947, *Jallu 5257* (LD), 1964, *7832* (LISE).

Early specimens from plants cultivated in Botanical Gardens:

Erlangen, Germany, Herb. *Schreber in 1779* (M). Paris, *in 1781* (MPU). Erlangen, Herb. *Schreber in 1800* (M). Halle, Germany, *Fischer in 1801* (L). Montpellier, France, *in 1808* (MPU). Hamburg, Germany, from seeds of the Botanical Garden Kiel, *in 1815* (HBG). Munich, Germany, Herb. *Zuccarini in 1835* (M; as *O. nervosa*). Paris, *Abbé Pouret in 1847* (P). Hort. Cantab., seeds from the Canary Islands, Herb. *Gray in 1867* (GH; as *O. canariensis*).

Oenothera longiflora reported in literature from outside of South America:

FRANCE: Gandoger (1886: 49); Rouy & Camus (1901: 201); Coste (1903: 81); Thellung (1912); Bonnier (1921: 29); Fournier (1937: 598); Issler, et al. (1965: 357); Raven (1968).

BELGIUM: Jean (1975).

PORTUGAL: Gandoger (1886: 49); Coutinho (1913: 427; 1939: 508); Raven (1968).

AZORES: Trelease (1897: 114).

MADEIRA: Lowe (1868: 275); Menezes (1914: 71).

SPAIN: Raven (1968).

SOUTH AFRICA: Phillips (1917: 99; as *O. villosa*); Adamson & Salter (1950: 606).

JAMAICA: Grisebach (1860: 273).

18. **Oenothera catharinensis** Cambess., in St.-Hilaire, Fl. Bras. Mer. 2: 270. 1829.—FIGS. 3, 53–54, 130.

O. mollissima sensu Munz, Amer. J. Bot. 22: 659. 1935, pro parte.

Erect annual herb, not forming a rosette, bushily branched near the base, 1–5 dm tall. Plants densely to sparsely strigillose and villous in the lower portions, densely to sparsely long-villous and thickly to sparsely glandular-pubescent elsewhere. Cauline leaves cultrate to narrowly lanceolate, acute, acute to rounded at the base, sessile, 3–5 cm long, 0.7–1 cm wide; bracts narrowly oblong to lanceolate, acute to rounded at the base, sessile, 2–4 cm long, 0.5–0.8 cm wide, mostly shorter than the capsules they subtend; leaves plane and irregularly serrate with blunt teeth. Inflorescence branched. Floral tube 3–4 cm long. Buds lanceolate in outline, 1.8–2.2 cm long, 5–6 mm thick, green or yellowish green; apices of the sepals erect, ca. 1.5 mm long. Petals very broadly obovate, retuse, 3–3.5 cm long. Anthers 7–10 mm long. Filaments 15–18 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 4–5.5 cm long. Stigma lobes 5–8 mm long. Ovary 1–1.5 cm long. Capsule 3–4 cm long, 3–4 mm thick. Seeds elliptic in outline, 1.5–1.8 mm long, 0.6–0.8 mm wide, brown. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 14** or ring of 4 and 5 bivalents*** at meiotic metaphase I). Flowering time: October–March.

Type: Brazil, Santa Catarina, Îlha Santa Catarina, Apr. (1816–1821), *Auguste de St.-Hilaire 1721* (P, holotype, F and GH photographs; MPU, P, isotypes).

Distribution (Fig. 229): Apparently only along the coast of the state of Santa Catarina, Brazil.

Specimens examined from cultivated plants:

BRAZIL. SANTA CATARINA: Coast near Itapema, *Hatschbach in 1971*** (DUSS, M, MO). Isle of Santa Catarina, Praias Inglese, *Conrad & Dietrich 8****, *9**, *10**, *13** (DUSS).

Additional specimens examined:

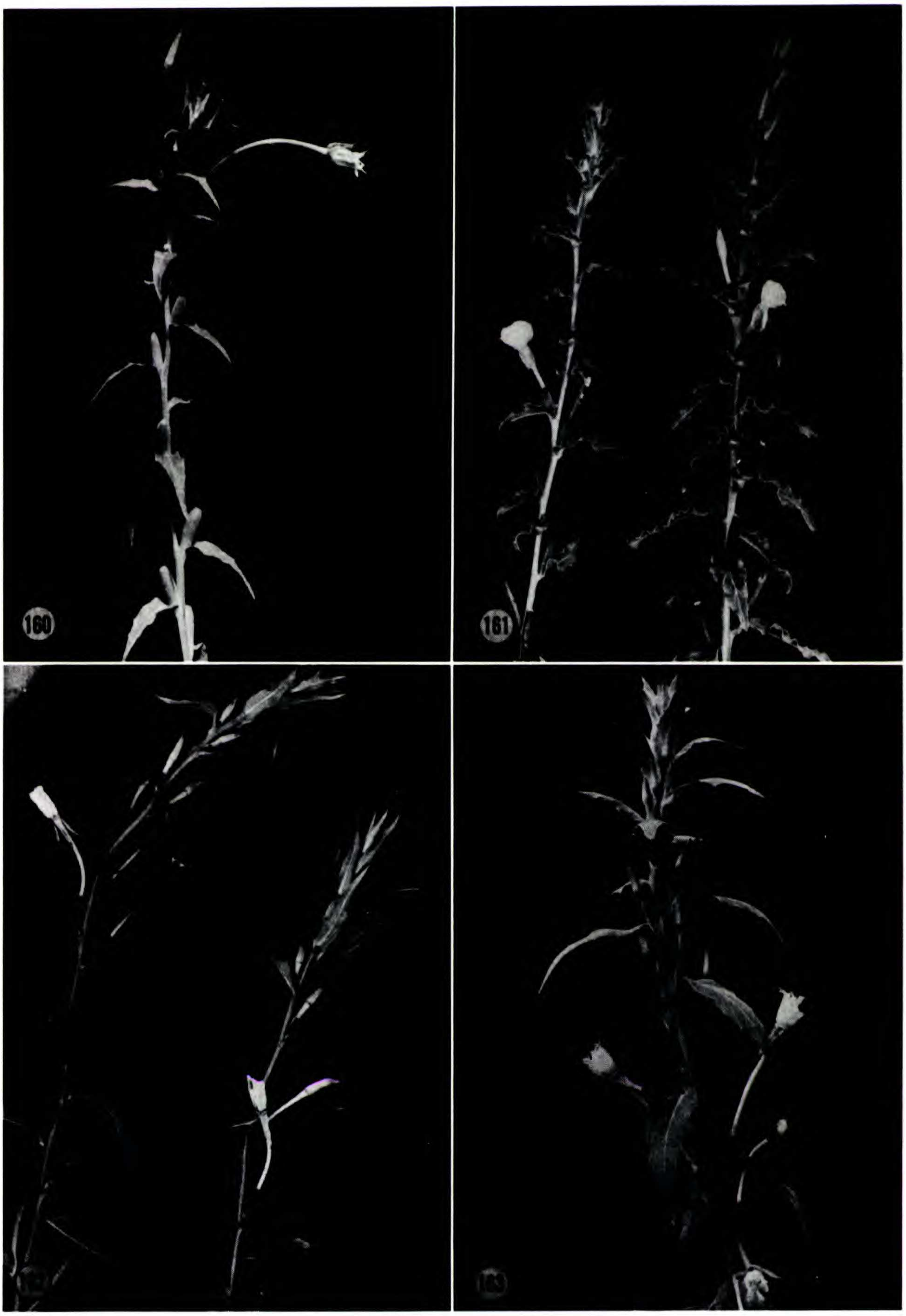
BRAZIL. SANTA CATARINA: Santa Catarina, *N.N.* (GOET). Isle of Santa Catarina, *Gaudichaud 252* (P). Isle of Santa Catarina, Pântano do Sul, *Klein et al. 5824* (HBR, RSA). Rio Vermelho, *Klein et al. 5801* (HBR, RSA); *Perdonnet 233* (G). Laguna, *Reitz & Klein 185* (RSA), *137* (HBR, RSA).

Oenothera catharinensis has generally been regarded as a synonym of the complex structural heterozygote *O. mollissima* (Munz, 1935), but it can be distinguished from that species by its strigillose pubescence, which is never present in *O. mollissima*, and its larger flowers. The pubescence, flower size, and short bracts of *O. catharinensis* indicate that it is a relative of *O. ravenii* rather than of *O. mollissima*.

I have been unable to discover any evidence that *O. catharinensis* has participated in the origin of any complex heterozygote. From this, I conclude that it may be a species of relatively recent origin derived from an ancestor similar to *O. ravenii* as an obligate annual strain with altered characteristics (Fig. 8). The occurrence of complex heterozygote strains with a ring of 14 chromosomes may reflect a situation similar to that in *O. affinis* and *O. odorata*.

19. **Oenothera indecora** Cambess. in St.-Hilaire, Fl. Bras. Mer. 2: 268. 1729.—FIGS. 2, 44–46, 131–132, 178–179, 215–217.

Erect annual, forming a rosette, unbranched or with a moderately or strongly branched main stem and arcuate to obliquely ascending side branches arising from the rosette, 2–6 dm tall. Entire plant sparsely long-villous with erect hairs, densely to sparsely short-villous, and densely glandular-pubescent; or only densely short-villous and densely glandular-pubescent. Rosette leaves narrowly oblanceolate, acute, gradually or ± abruptly narrowed to the petiole, 4–8 cm long, 0.2–1.3 cm wide; cauline leaves very narrowly elliptic to lanceolate, acute, acute at the base, sessile, 2.5–7 cm long, 0.2–1.2 cm wide; bracts very narrowly elliptic to elliptic, acute, acute at the base, sessile, longer than or about the same length as the capsules they subtend, 1.5–5 cm long, 0.2–1 cm wide; leaves plane or undulate at the margins, irregularly serrate with blunt teeth. Inflorescence branched. Floral tube 0.5–1.5 cm long. Buds oblong to broadly elliptic in outline, 0.2–0.8 cm long, 1.5–4 mm thick. Sepals green or yellowish green, often ± densely flecked with reddish brown; apices of the sepals 0.5–1 mm long, erect. Petals broadly elliptic to very broadly obovate, yellow or bright yellow, 4–10 mm long. Anthers 1.5–4 mm long. Filaments 1.5–7 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1–2 cm long. Stigma lobes 1–2 mm long. Ovary 1–1.5 cm long. Capsule 2–3 cm long, 1.5–2 mm thick. Seeds broadly elliptic to rotund in outline, 0.7–1.3 mm long, 0.3–0.5 mm thick. Cleistogamous, almost always fertilized in bud. Gametic chromosome number, $n = 7$ (7 bivalents or ring of 14 at meiotic metaphase I).



FIGURES 160–163. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—160. *O. pseudoelongata* (Bolivia, Cochabamba, *Santarius 1988*).—161. *O. cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—162. *O. siambonensis* (Argentina, Tucumán, *Göpel in 1961*).—163. *O. brevipetala* (Bolivia, Cochabamba, *Santarius 1972*).

Type: Brazil, Rio Grande do Sul, sandy places near the farm Manguiera, not far from the city of Rio Grande, Aug. (1816–1821), *Auguste de St. Hilaire 1872 bis* (P, holotype, F and GH photographs; MPU, P, isotypes).

Distribution (Fig. 231, 233): In Brazil from the states of São Paulo to Rio Grande do Sul; in Uruguay in the departments of Cerro Largo, Treinta y Tres, Rocha, Maldonado, Montevideo, San José, Ártigas, Riviera, Salto, and Río Negro; in Argentina throughout the northern and eastern portions of the republic, in the provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, Formosa, Chaco, Santiago del Estero, Santa Fé, Córdoba, San Luis, Misiones, Corrientes, Entre Ríos, and Buenos Aires; in central Paraguay; and in Bolivia in the vicinity of La Paz (subsp. *boliviensis*).

Together with *O. mendocinensis* and *O. verrucosa*, *O. indecora* contradicts the rule that chromosomally homozygous entities in the genus are usually large-flowered. In comparison with *O. mendocinensis*, *O. indecora* has wider leaves, shorter capsules, smaller seeds, and never any strigillose pubescence.

KEY TO THE SUBSPECIES

1. Plants exclusively short villous and glandular-pubescent, appearing glabrous to the naked eye.
    2. Bracts 0.5–1.3 cm wide; buds 4–8 mm long; petals 0.5–1 cm long .... 19b. subsp. *bonariensis*
    2'. Bracts 1.5–2 mm wide; buds 2–3 mm long; petals 0.2–0.3 cm long .... 19c. subsp. *boliviensis*

1'. Plants sparsely long villous, densely short villous, and densely glandular-pubescent, appearing pubescent to the naked eye; bracts 0.5–1 cm wide; buds 3–8 mm long; petals 0.4–1 cm long .... 19a. subsp. *indecora*

19a. **Oenothera indecora** subsp. **indecora**.—Figs. 131, 178, 215–216.

Onothera polymorpha H. Lév. race *mollissima* (L.) H. Lév. var. *indecora* (Cambess.) H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909.

Raimannia indecora (Cambess.) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.

Oenothera argentinae H. Lév. & Thell. var. *longipila* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherlands, Weert, oatfield near the Karelke meal factory, 13 Aug. 1920, *A. W. Kloos* (L-95264486; BAS, isolectotype).

Plants 2–4 dm tall. Entire plant sparsely long-villous, densely short-villous, and densely glandular-pubescent. Rosette leaves and cauline leaves 5–7 cm long, 0.5–1 cm wide; bracts 3–5 cm long, 0.5–1 cm wide. Buds 0.3–0.8 cm long, 2.5–4 mm thick. Sepals ± densely flecked with reddish brown, seldom immaculate. Petals 0.4–1 cm long. Anthers 2–3 mm long. Filaments 3–6 mm long. Seeds elliptic in outline, 1–1.3 mm long, 0.4–0.5 mm thick. Cleistogamous. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: Brazil, September–July; Uruguay, Paraguay and Argentina, September–May.

Distribution (Fig. 231): In Brazil from the states of São Paulo to Rio Grande do Sul; prevalent in the coastal departments of Cerro Largo, Treinta y Tres, Rocha, Maldonado, Montevideo, Colonia, Canelones and San José in Uruguay, and also in the departments of Ártigas, Salto, Lavalleja and Rivera; in Argentina known from the provinces of Misiones, Corrientes, Entre Ríos, Formosa, Chaco and Córdoba; in Paraguay only from Encarnación in the southeast of the country.

Specimens examined from cultivated plants:

URUGUAY. MALDONADO: Sandy places in the southern part of Piriapolis, *Santarius 147, 150*, 151, 152, 153*, 155, 156* (DUSS; *150* also CTES; *150, 152* also M, MO). FLORIDA: At the railroad 1–3 km NE and SW of Mansavillagra, *Santarius 205*, 206*, 208*, 209*, 212*, 213** (DUSS; *205, 208, 209* also CTES, M; *205, 206, 208, 209* also MO). Lavadero San Pedro, *Hecht 1964-63** (DUSS, M, MO).

Additional specimens examined:

BRAZIL. SÃO PAULO: Pinheiros, *Gehrt 34390* (POM, SP). PARANÁ: Curitiba, *Hoehne 23080* (POM, SP). Pôrto Vitória near Curitiba, *Hatschbach 1-1969* (UC). SANTA CATARINA: Itajai, *Klein 2567, 2686* (HBR, RSA); *Mueller s.n.* (R), *397* (K). Near Palmitos, 400 m, *Smith & Reitz 12584* (HBR, US). Rio Irani 12 km S of Faxinal des Guedes, 500–600 m, *Smith & Klein 12903* (HBR, RSA). Rio Uruguai near Itapiranga, 200 m, *Smith & Klein 13184* (HBR, RSA). Ilha de Santa Catarina, *Klein & Bresolin 8338* (HBR). Araranguá near Sombrio, *Reitz C748* (BR, HBR). Pirão Frio near Sombrio, 10 m, *Reitz & Klein 9072* (HBR). Est. Exp. de Videira, *Santos 2894* (R). Tubarão near Laguna, *Ule 1256* (HBG, P). RIO GRANDE DO SUL: Near Trés de Maio, *Santos 2763* (R). Serro de Pustral near Sta. Maria, *Vidal 01199* (R). Palmeira near Xingu, 650 m, *Bornmüller 745* (GH). São Sepé near Cacapava, *Rosengurtt 8734* (MVFA). City of Rio Grande, *Malme 270* (S). Viera, *Archer 36795* (SP), *4301* (BR, GH, NY, POM, US). Between Pelotas and Rio Grande, *Krapovickas & Cristóbal 22901* (MO). Pelotas, *da Costa Sacco 1116* (F, HBR); *Casagrand et al. 13* (CTES). Facenda Saledade near Rio Pardo, *Jürgens 25, 97* (B); *Vidal 01526, 01533* (R). Montenegro near L. S. Pedro, *Sehnem 3833* (B, SI). San Leopoldo, *Reuter in 1953* (R); *Eugenio 201, 206* (NY); *Rambo 293* (LIL). Uruguayana, *Palacios & Cuezzo 202, 227* (LIL); *Vidal 01315, 01318* (R). Passo de Ricarde at Rio Piratini, *Pereira 6773* (RB). Toca do Tigre near Itapoan, *Rambo 48931* (LIL, MO), *48934* (HBR, RSA). Pôrto Alegre, *Rambo 293* (SP). Gloria near Pôrto Alegre, *Rambo 978* (SP), *27196* (LIL, S), *28995* (RSA, LIL). Villa Manresa near Pôrto Alegre, *Rambo 37466* (F, HBR, LIL, RSA), *57073* (HBR), *55570* (B, HBR). Balneario Ipanema near Pôrto Alegre, *Emrich 1126* (LIL). São João near Pôrto Alegre, *Reineck & Czermak 30* (HBG). Praia Tramandahy near Pôrto Alegre, *Vidal in 1913* (R). Montenegro, *Rambo 29702* (LIL). Pareci near Montenegro, *Rambo 29702, 42445* (LIL). Amaral Ribeiro near Taquara, *Rambo 42391* (F, LIL). Travessão near Hamburgo, *Rambo 42181* (LIL). Osorio, *Rambo 48887* (LIL). Morro Sapucaia near Pôrto Alegre, *Rambo 37381* (SI). Est. Azevedo, *Rambo 43276* (LIL).

URUGUAY. ÁRTIGAS: Cuareim, *Berro 2319* (MVFA). Santa Amaro, *Jürgens 168* (B). SALTO: Dayman, *Osten 5258* (SI, US). RIVERA: Cuñapiru, 200–230 m, *Wright in 1928* (BM). FLORIDA: Mansavillagra, *Rosengurtt B790* (POM). SAN JOSÉ: Sierra Mahoma, *Izaguirre 2591* (MVFA). Rincón del Pino, *Izaguirre 9543* (MVFA). COLONIA: Between Colonia and Montevideo, *Burkart 29012* (SI). MONTEVIDEO: Carrasco, *Rosengurtt 861* (POM); *Berro 7550* (MVFA). Sta. Lucía, *Fruchard 788* (P). CERRO LARGO: Est. Perdomo near Ruta 8 and Arroyo Tacuari, *Arrillaga 2358* (F). Between Río Negro and Acegua, *Rosengurtt 851a* (POM). TREINTA Y TRES: Km 323 at Ruta 8, *Marchesi 2268* (MVFA). LAVALLEJA: La Lorenzita, *Lombardo 9132* (MVFA). Abra de Perdano, *Olano 8838* (MVFA). Cerro Arequita near Minas, *Krapovickas & Cristóbal 16149* (CTES). CANELONES: Sta. Lucía, *Gibert 988* (K); *Felippone 5574, 5589* (SI). ROCHA: La Coronilla, *Brescia 3984* (MVFA). Parque Sta. Tereza, *Rodriguez 8146* (MVFA). MALDONADO: Sierra de las Animas, *Izaguirre 10751* (MVFA). Cerro Pan de Azúcar, *Bartlett 21003* (GH, MICH, UC, US).

PARAGUAY. Encarnación, *Hassler 1476* (SI); *Bertoni 4532* (LIL).

ARGENTINA. MISIONES: Bonpland, *Van de Venne 275* (POM). Montecarlo, *Schinini 5493* (CTES). CORRIENTES: Dep. Mercedes, at Río Miriñay near Ruta 23, *Schinini et al. 7124* (CTES, MO). ENTRE RÍOS: Concepción del Uruguay, *Lorentz 424 pro parte* (GOET); *Burkart 28762* (MO). Between Colón and Concepción, *Burkart 28991* (MO). San Salvado, *Baez 52972* (BAB). Arroyo Maimol near Colón, *Nicora 3238* (LIL). Km 249 at Ruta 14 near Concrodia, *Burkart 22664* (MO). Arroyo Isletas, *Burkart 27034* (MO). Paraná, *Burkart 23759* (MO); *Anetto in 1891–92* (CORD). Gualeguaychi, *Meyer 10331* (LIL). Médanos, *Burkart 3470* (POM). Río Tale, *Schulz 284* (LIL). Paranacito, *Ragonese 6* (BAB). FORMOSA: *N.N. in 1904* (SI-4860). Reventón near Pilcomayo, *Morel 1913* (LIL). CHACO: Dep. Independencia, Campo Largo 8 km from J. Mármol, *Bacigalupo et al. 9601* (BAA, MO, SI), *9604* (BAA). Puerto El Colorado, *Rojas 12113* (LIL). Dep. Napalpi, C. del Bermejo, *Burotorich 535* (LIL).

CÓRDOBA: Vicinity of Alta Gracia, *Hunziker 7710* (CORD). Sierra Ochoa near Sta. María, *Stuckert 13562* (CORD). Between Est. Burmeister and Onagoity near Gral. S. Martín, *Di Fulvio 21411* (CORD). At km 571 of Ruta 35 between Huinca Renancó and Río Quinto, *Hunziker & Di Fulvio 21430* (CORD). Near Copina, *Hunziker 6951* (CORD).

Specimens from outside of South America:

NETHERLANDS. Wormerveer, meal factory, *Jansen & Kloos in 1913* (BAS).

FRANCE. Dép. Nord, Dunkerque, *Bouly de Lesdain in 1924* (BAS).

HUNGARY. Györ at river Danube, 1916, *Polgar 2468* (BAS).

Plants intermediate between *O. indecora* subsp. *indecora* and *O. indecora* subsp. *bonariensis* are occasional in the zone of overlap between these two entities and may be recognized by the fact that they are only sparsely long villous. All plants of this species are in effect cleistogamous, fertilization taking place in bud well before the unfolding of the flowers; and this factor alone must drastically limit the possibility of hybridization and thus help to maintain the integrity of the two subspecies where they come together.

One of the genomes of the complex heterozygote *O. montevidensis* is derived from *O. indecora* subsp. *indecora*.

19b. **Oenothera indecora** subsp. **bonariensis** Dietrich, subsp. nov.—FIGS. 2, 44–46, 132, 179, 217.

Oenothera humifusa Torr. & A. Gray f. *erecta* Thell. & Zimmerm., Repert. Spec. Nov. Regni Veg. 14: 375. 1916. TYPE: Germany, port of Ludwigshafen, Sep. 1909, *F. Zimmermann* (BAS).

Onothera argentinae H. Lév. & Thell. ex H. Lév., Monde Pl., sér. 2, 18 (108): 52. 1917; H. Lév. & Thell., Repert. Spec. Nov. Regni Veg. 15: 133. 1918. LECTOTYPE: Germany, dockyard of Uerdingen at the Rhine near an oil refinery, 26 Sep. 1915, *Bonte* (Z; BA, POM, isolectotypes). Léveillé's mention of *Onothera argentinae* in Monde Pl., sér. 2, 18 (108): 52. 1917, is not a nomen nudum, as stated by Lauener (1972: 424).

O. argentinae var. *typica* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherlands, Rotterdam, Maashaven meal factory, 10 Sep. 1920, *A. W. Kloos* (L-954264523; BAS, isolectotype).

O. argentinae var. *brevipila* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherland, Weert, oatfield near the Karelke meal factory, 13 Aug. 1920, *A. W. Kloos* (L-954264489; BAS, isolectotype).

O. indecora sensu Munz, Physis 11: 281. 1933, pro parte; Amer. J. Bot. 22: 658. 1935, pro parte; sensu Munz, Fl. Brasílica 9(41): 53. 1947, pro parte.

O. argentinae "Erlangen" Haustein, Z. Indukt. Abstammungs- Vererbungsl. 84: 418. 1952.

O. indecora "Argentinae," "Buenos Aires" and "Reconquista" Cleland, Jap. J. Genet. 43: 332. 1968.

Plantae 2–6 dm altae, ubique dense breviter villosa denseque glanduloso-pubescentes, sine lente ut videtur glabrae. Folia rosulae 5–7 cm longa, 0.5–1.3 cm lata; bractea 3–5 cm longa, 0.5–1.3 cm lata. Gemmae 0.4–0.8 cm longae, 2.5–4 mm crassae. Sepala viridia vel flavovirentia, raro rubro. Semina ambito late elliptica, 0.7–1 mm longa, 0.4–0.5 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica vel heterozygotica complexa.

Plants 2–6 dm tall. Entire plant densely short-villous and densely glandular-pubescent, apparently glabrous when viewed without a lens. Rosette leaves 5–7 cm long, 0.5–1.3 cm wide; bracts 3–5 cm long, 0.5–1.3 cm wide. Buds 0.4–0.8 cm long, 2.5–4 mm thick. Sepals green or yellowish green, rarely flushed with red. Petals 0.5–1 cm long. Anthers 1.5–4 mm long. Filaments 4–7 mm long. Seeds broadly elliptic in outline, 0.7–1 mm long, 0.4–0.5 mm thick. Self-polli-

FIGURES 164–165. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—164. *O. acuticarpa* (Argentina, Tucumán, *Göpel in 1961*).—165. *O. tucumanensis* (Argentina, Tucumán, *Santarius 1657*).

nating and often cleistogamous. Gametic chromosome number, $n = 7$ (7 bivalents* or ring of 14** at meiotic metaphase I). Flowering time: September–July.

Type: Argentina, Prov. Buenos Aires, Isla Santiago near La Plata, 24 Nov. 1935, *A. L. Cabrera 3406* (NY, holotype; F, G, LIL, LP, POM, SI, UC, isotypes).

Distribution (Fig. 233): In Brazil from the state of São Paulo to Rio Grande do Sul; in Uruguay the stations are all in the western and southwestern departments of Río Negro, San José, and Florida; in central Paraguay and throughout the range of the species in Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: On sandy soil of Isla Santiago near La Plata, *Santarius 275**, *276**, *277**, *278**, *281**, *284**, *285*, *287*, *291**, *292*, *295*, *297*, *299* (DUSS; *275* also CTES, M, SP; *275*, *276*, *277*, *278*, *284* also MO). Buenos Aires, *Cleland 1967-508** (CTES, DUSS, MO). TUCUMÁN: Rio Salí near Tucumán, "El Cadillal," *Göpel in 1961** (DUSS, MO). CORRIENTES: Santo Tomé, *Krapovickas 16404* (DUSS, MO).

URUGUAY. COLONIA: Sandy places at roads in western part of Juan L. Lacaze, *Santarius 68***, *72* (DUSS; *68* also M, MO).

BRAZIL. PARANÁ: Corredeira Paulista at Rio Jaguariaiva near São José da Bôa Paulista, *Hatschbach 25564* (DUSS).

CULTIVATED: *O. argentinae* from Erlangen, Germany, received 1960* (CTES, DUSS, M, MO).

Representative specimens examined:

BRAZIL: SÃO PAULO: Alto da Serra, *Gehrt 39948* (POM, SP). PARANÁ: Curitiba, *Dusén 13292* (F, MO, S), *2219* (R), *15827* (GH, LE, NY, S). Jaguariaiva, *Dusén 13189* (S, SI). SANTA CATARINA: Itajai, *Klein 6859* (HBR, RSA). Nova Teutonia, *Plaumann 583* (RB). RIO

GRANDE DO SUL: Uruguaiana, *Vidal 01328* (R). Rio Grande, *Malme 110* (S). Rio Pardo, *Jürgens in 1923* (B). Pôrto Alegre, *Lindmann 363* (S).

URUGUAY. RÍO NEGRO: Near Mercedes, isles of Río Negro, *Rosengurtt 855* (POM). SAN JOSÉ: Río Santa Lucía, *Rosengurtt 859* (POM). FLORIDA: La Palma, *Herter 2105* (F, MO, US, Z).

PARAGUAY. Villarica, *Jörgensen 4117* (C, F, MO, NY, S, SI, US). Villa Elisa near Asunción, *Pedersen 5118* (C). Botanical Garden of Asunción, *Rojas 3174* (POM). Asunción, *Balansa 2219* (K, P, RSA). Sierra de Maracayú near river Capibary, *Hassler 4409* (BM, K, NY, P, UC, W). Sma. Trinidad, *Zürcher in 1913* (Z). Without exact locality, *Bonpland in 1833* (P).

ARGENTINA. BUENOS AIRES: Tigre near Garín, *Lanfranchi 485* (LP). El Socorro near Pergamino, *Parodi 7401* (GH). Campana, *Krapovickas 2593* (BAB, LIL); *Hunziker 1044* (CORD, LIL, RSA). Juinez, *Molfino 146* (POM). Est. Las Palmas near Port. Zárate, *Boelcke 13152* (BAA). Villa Ortuzor, *Parodi 9900* (K, POM, US). Isla Paulino, *Cabrera 7385* (F, GH). Ramalla at Río Paraná, *Burkart 12767* (SI). Pavón at Río Paraná, *Pennington 171* (CORD). Isla Maciel, *Krapovickas 222* (LIL). Federación, *Birabén 5127* (LP). MISIONES: Villa Venecia near Leandro N. Alem, *Krapovickas & Cristóbal 15970* (BAB, CTES, MO). Deseado near Frontera, *Pierotti 5248* (LIL). 20 km S of Bernardo de Irigoyen, 150 m, *Krapovickas & Cristóbal 13714* (BAB, C, CTES, UC). Puerto Polana near Cainguas, *Schwarz 7920* (LIL). Corpus, *Scala* 257 (LIL). Santa Ana, *Rodriguez 647* (GH, LIL, POM, SI, UC). Orera near Candelaria, *Pierotti 5265* (LIL). Loreto near Candelaria, *Montes 14665* (NY). Garupá near Candelaria, *Bertoni 2377* (BM, F, LIL, S). Puerto Cazador near San Ignacio, *Schwartz 4900* (LIL). Posadas, *Grondona & Spegazzini 1111* (BAB). Puerto Istuela near Iguazú, *Montes 9291* (GH, LIL). Eldorado near Iguazú, *Schmidt 2097* (LIL). Apóstoles, *Krapovickas et al. 15485* (CTES). CORRIENTES: Paso de la Patria near San Cosmé, *Tressens et al. 119* (BAA, CTES, F, LP, MO); *Ibarrola 775* (LIL, NY). San Luis de Palmar, *Ibarrola 3260* (LIL). Laguna Rincón near Gral. Paz, *Schwarz 8554* (LIL). Loma Alta near Ituzaingó, *Pierotti 600* (LIL). Between Río Empedrado and Ruta 12, *Quarín & Schinini 1297* (CTES, MO). Est. "Ita Caabó" near Mercedes, *Pedersen 6159* (C, GH, K, US). Est. "Santa Teresa," *Pedersen 117* (P, S, US). Santa Ana, *Parodi 12061* (BAA). Dep. Capital, between Arroyo Riachuelo and Ruta 12, *Krapovickas & Cristóbal 13559* (CTES, MO). Tabay near Concepción, *Krapovickas & Cristóbal 11709* (CTES, K, US). Loreto near San Miguel, *Mroginski 42* (CTES). Laguna Mansa near Paso de los Libres, *Schinini 7603* (CTES, MO). ENTRE RÍOS: Paraná, *Boelcke 1268* (BAA). Isla del Pillo near Victoria, *Burkart 8735* (F, POM). Colón, *Burkart 24874* (MO). Ibicuycito, *Burkart 27309* (MO). San Carlos near Concordia, *Crovetto & Grondona 4139* (BAB). Delta del Paraná, Arroyo Martinez, *Boelcke 901* (BAA). Federación, *Meyer 11131* (LIL). FORMOSA: Colonia Pastoril, *N.N. 98* (BAB). CHACO: Margarita Belén, *Aguilar 1078* (LIL); *Stuckert 19370* (CORD). Las Palmas, *Jörgensen 2489* pro parte (POM). Fontana, *Meyer 455* (LIL, POM, SI). Vis-a-vis of Corrientes, *Alboff in 1890* (NY). Colonia Benítez, *Schulz 502* (POM), *10075* (BAB). SANTA FÉ: Mocoví, *Venturi 94* (BAB, CORD, LIL, P, POM, SI). Guadalupe, *Huidobro 3389* (LIL, RSA). Esperanza near Las Colonias, *Huidobro 3263* (LIL, RSA). Colonia Mascías near Garay, *Pueyo 105* (CTES). Rosario, *Burkart 8772* (F, SI). Laguna Setubal, *Alvarez 807* (LIL). San José del Rincón, *Alvarez in 1916* (LIL). San Justo, *Erbaggi & León 966* (SI). San Cristóbal, *Balegno 593* (LIL). Reconquista, *Parodi 11129* (POM), *11146* (BAA, POM); *Burkart 5795* (F, SI). SANTIAGO DEL ESTERO: Colonia Jaimez near Robles, *Luna 1329* (LIL); *Ruiz in 1948* (RSA). Zurena near Robles, *Maldonado 441* (LP). La Isleta between Ceres and Colonia near Rivadavia, *Hunziker 10384* (CORD). Selva near Rivadavia, *Balegno 462* (LIL). Parque Aguirre in Santiago del Estero, *Argañaraz 440* (LIL). El Puestilo near Guasayán, *Cuezzo 2405* (LIL). La Banda, *O'Donell 4248* (LIL). CÓRDOBA: *Hieronymus in 1878* (BR, FR, K, LE, P). San Vicente, *Kurtz 576, 577* (CORD). Río Primero, *Kurtz 2625* (CORD). Capilla del Monte, *Hossens 364* (CORD). Emp. Tanti near Punilla, *De la Sota 3075* (LIL). Río Segundo, *Sublis 1080* (CORD). Ascasubi near Tercero Arriba, *Krapovickas 6391* (BAB, CORD). Cárcano near San Martín, *Krapovickas 7403* (LIL). Casa Bamba near Colón, *Stuckert 23732* (CORD). Near Villa Dolores, *Hunziker 13204* (RSA). Alta Gracia, *Hunziker 6761* (CORD, LIL). Est. La Redución in the Sierra Chica, *Pastore 348* (SI). SAN LUIS: *Burkart 12086* (SI). JUJUY: Agua Negra near Ledesma, *Fabris et al. 3044* (LP). Villa Achaval, *Cabrera 20059* (LP). SALTA: Río San Francisco near Orán, *Rodríguez 1155* (GH, LIL, POM, SI). Puerta Verde near Santa 2° sección, *N.N. 603* (LIL-216719). Vallecito near Metán, *Lenna 384* (LIL). TUCUMÁN: Cerro San Javier, *Boelcke 2911* (BAA, MO). Río Salí, *Venturi 898* (BAA, GH, LIL, POM, SI, US). Chañar Pogo near Leales, *Venturi 491* (LIL, LP, MO, POM, SI). Agua Dulce near

Leales, *Monetti 1163* (GH, LIL). Río Colorado near Famaillá, *Carenzo 3425, 2429* (LIL). Yerba Buena, *Meyer in 1949* (LIL). El Morado near Burroyacú, *Peirano 10085* (LIL). CATAMARCA: Andalgala, *Jörgensen 1054* pro parte (LIL). Choya near Andalgala, *Castillon 14417* (GH, LIL). San Antonio, *Castillon 1283* (LIL). Río del Valle near Piedra blanca, *Lillo 9085* (LIL). LA RIOJA: Quebrada de Soria, 8 km SE of Chamical, *Hunziker 16638* (CORD). Nonogasta, *Castellanos 27-2011* (POM). F. Belgrano, *Gomez 66* (LIL). Dique de Alta, *Hunziker & Fabris 14441* (CORD). SAN JUAN: Valle Fertil, *Hunziker 16698* (CORD).

Specimens from outside of South America (naturalized):

GERMANY. Humboldt mill near Tegel, Berlin, *Schulz in 1896* (B). Port of Ludwigshafen, *Zimmermann in 1907* (L). Port of Neuss, *Bonte in 1926* (BAS). Finkenwerder near Hamburg, *Christiansen in 1926* (BAS). Emmerich, 1930, *Kern & Reichgelt 12180* (L).

NETHERLANDS. Wormerveer, 1913, *Kloos 57* (L), *in 1916* (L), *in 1923* (L). Rotterdam, 1904, *Jansen & Wachter 13287* (L), *in 1920* (L); *Kloos in 1920* (BAS, L).

FRANCE. Dép. Nord, Dunkerque, 1926, *Bouly de Lesdain 585* (BAS).

PORTUGAL. Barreiro near Estremadura, 1958, *Rainha 3703* (LISE). Moita, 1961, *Rainha 4844* (LISE).

RHODESIA. Distr. Selukwe, Ferny Creek, ca. 1,190 m, 1953, *Wild 4281* (K, MO, SRGH); 1966, *Biegel 1498* (SRGH). Distr. Gwelo, 1,280 m, 1965, *Biegel 475* (SRGH).

BOTSWANA, Distr. South Eastern, Gaberone, Content Farm, 1972, *Kelaole A 78* (SRGH).

SOUTH AFRICA. TRANSVAAL: Near Pretoria, 1930, *Moss 18261* (BM). Distr. Letaba, 1958, *Scheepers 270* (BM, K, MO, PRE, SRGH). Duiwelskloof, 945 m, 1958, *Scheepers 270* (K). Distr. Wolmaranstad, *in 1963* (PRE-29488). Pta. Harde near Eloffsdal, 1963, *Hanekom 1663* (K, SRGH). NATAL: Distr. Ifafa River, ca. 610 m, 1948, *Gerstner 6932* (PRE). Distr. Port Shepstone, St. Michaels-on-Sea, 1966, *Strey 7094* (K). Distr. Umzinto, Shelley beach, 1967, *Strey 7284* (K). ORANJE FREE STATE: Bloemfontein, 1956, *Gemmell 6737* (K). Distr. Swinburne, Rensburgshop, 1961, *Jacobsz 91* (PRE). Distr. Kimberley, ca. 1,220 m, 1961, *Leistner 2931* (K, PRE). Distr. Frankfort, *Strydow* (K, PRE). LESOTHO: Maseru, 1969, *Williamson 22* (K, SRGH). CAPE: Hout Bay near Rondebosch, 1932, *Adamson 2198* (BM). Cape Peninsula, 1933, *Salter 4001* (K). Kuils River, near Bellville, 1953, *Parker 4849* (K). Stellenbosch, 1952, *Parker 4839* (K); 1964, *Taylor 5643* (K).

SOUTH WEST AFRICA: Windhoek mountains, Grundschwel near Finkenstein, 2,000 m, 1965, *Seydel 4223* (MO).

TRISTAN DA CUNHA: *Stableford in 1953-54* (K).

AUSTRALIA. NEW SOUTH WALES: Birdwood near Yarras, *Noonen in 1961* (NSW-135161). "Carp View" near Gilgandra, *Holawich in 1965* (NSW-135156). La Peraouse, *Coveny in 1965* (NSW), *in 1966* (NSW-135166). Morpeth, 1972, *Johnson 7538* (NSW).

Oenothera indecora subsp. *bonariensis* reported in literature from outside of South America:

SOUTH AFRICA: Jacot-Guillarmod (1971); Ross (1972: 262).

GERMANY: Léveillé & Thellung (1918).

FRANCE: Fournier (1937: 598, as *O. argentinae*).

Hybrids between *O. indecora* subsp. *bonariensis* and *O. stricta* subsp. *stricta* occur in Australia and Portugal.

AUSTRALIA. NEW SOUTH WALES: Warialda, *Lanagan in 1950* (NSW-135159). Casino Distr., *Glenfield in 1950* (NSW-135162). Narraben, *Mair in 1953* (NSW-68289). Patagona Beach, *Coans in 1954* (NSW-66109). Grafton, *Flynn in 1954* (NSW-66107). Warialda, *Grullan in 1956* (NSW-135158). Grafton, *O'Grady in 1957* (NSW, RSA). Moree Distr., *Mactier in 1962* (NSW-135155). Premer, *N.N. in 1962* (NSW-135157). Ashford, *McNamara in 1963* (NSW-135160). Menangle Park, 1964, *McBarron 9507* (NSW). Sackville Reach near Hawkesbury River, *Walker in 1965* (NSW-135164). Dee Why Laggon, *Coveny in 1966* (NSW-126453). Narrabeen Lake, *Coveny in 1966* (NSW-135165). Near Iluka, ENE of Maclean, 1969, *Coveny 2178* (NSW, DUSS).

PORTUGAL. ESTREMADURA: Moita, 1954, *Rainha 2703* (COI, LISE), 1961, *Rainha 4847* (LISE); Caldas da Rainho, 1960, *Rainha 4425* (COI, LISE); Costa da Caparics, *Matos in 1967* (COI).

Despite its extensive range, *O. indecora* subsp. *bonariensis* is very uniform, in contrast, for example, to *O. odorata* with its seemingly endless variability. This might be related to the great ecological amplitude of *O. odorata* and the

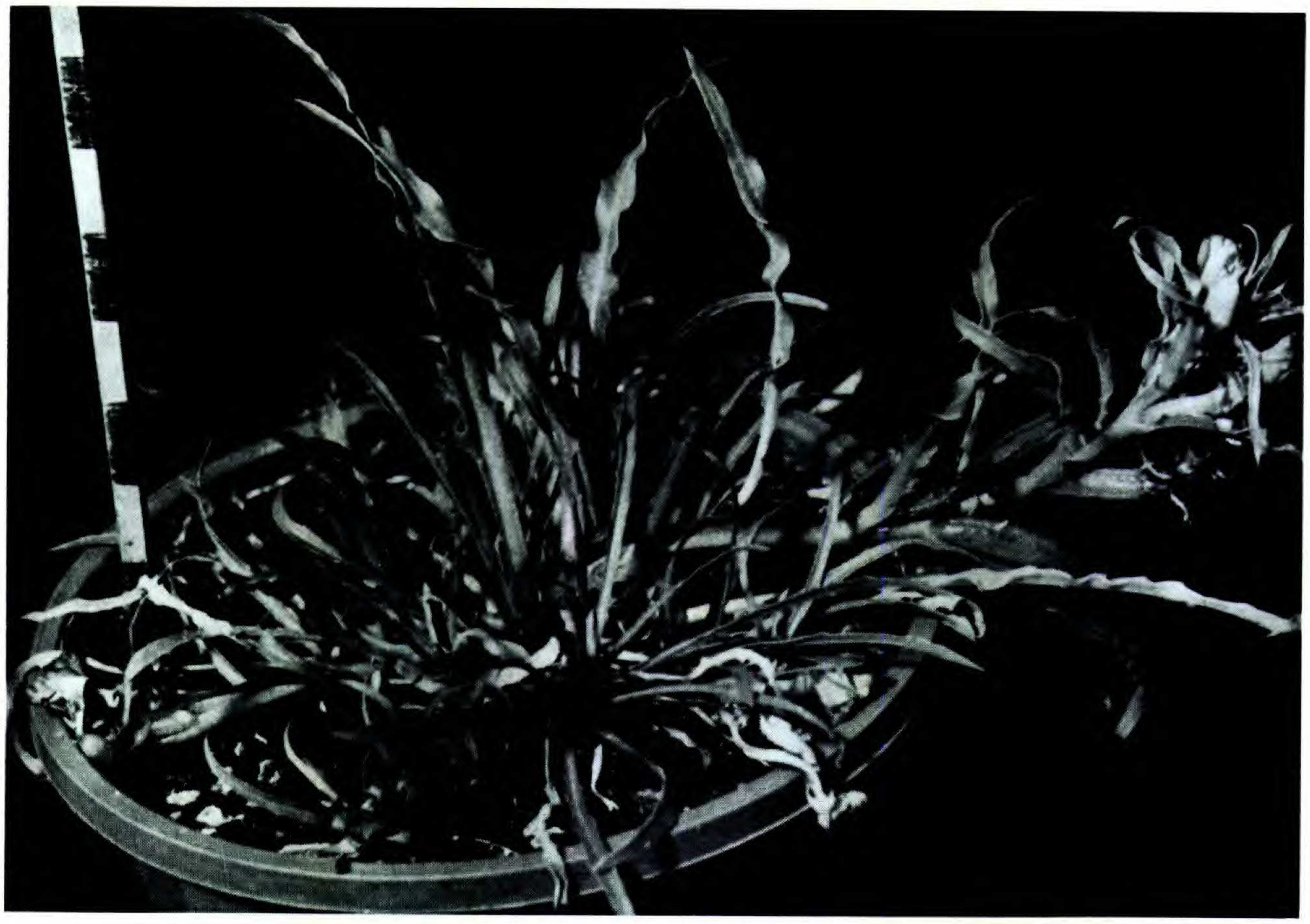


FIGURE 166. *Oenothera punae* (Bolivia, La Paz, *Santarius 2013*); *Oenothera* sect. *Oenothera* subsect. *Munzia*.

much more limited range of habitats in *O. indecora* subsp. *bonariensis*, which flourishes only in sandy places.

At least a major portion of the chromosomal complex of *O. indecora* subsp. *bonariensis* is represented in the chromosomally heterozygous entities *O. picensis* subsp. *bonariensis* and *O. parodiana* of series *Allochroa*, as well as in *O. brevipetala*, *O. tucumanensis*, and *O. punae* of series *Clelandia*.

The chromosomal heterozygotes from Uruguay (*Santarius 68, 72*) have two complexes derived within *O. indecora*. The relatively short bracts of these plants suggest, however, that one of these complexes may be modified by genes from *O. ravenii*, probably transmitted to *O. indecora via* the small-flowered *O. parodiana*.

19c. **Oenothera indecora** subsp. **boliviensis** Dietrich, subsp. nov.

Plantae maxime ad 20 cm altas, bene ramosae. Pubes ut in subsp. *bonariensis*. Folia caulina 2–3 cm longa, 2–3 mm lata; bractea 1.5–2 cm longa, 1.5–2 mm lata. Gemmae 2–3 mm longae, 1.5–2 mm crassae. Petala 2–3 mm longa. Capsula 1.5–2 cm longa. Semina ambito elliptica, 0.8–1 mm longa, 0.3–0.4 mm crassa. Cleistogama. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Plants attaining a height of only 20 cm, bushy and well branched. Pubescence as in subsp. *bonariensis*. Cauline leaves 2–3 cm long, 2–3 mm wide; bracts 1.5–2 cm long, 1.5–2 mm wide. Buds 2–3 mm long, 1.5–2 mm thick. Petals 2–3 mm long. Anthers 1.5–2 mm long. Filaments 1.5–2.5 mm long. Capsule 1.5–2 cm long. Seeds elliptic in outline, 0.8–1 mm long, 0.3–0.4 mm thick. Cleistogamous. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I).

Type: Cultivated in the Botanical Garden of Düsseldorf, Germany, 8 Aug. 1972. Source: Bolivia, near La Paz, A. *Hecht 1964-29* (MO-2155715, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 233): Known only from the type locality.

Specimen examined from cultivated plants:
BOLIVIA. LA PAZ: La Paz, *Hecht 1964-29** (CTES, DUSS, M, MO).

This subspecies seems clearly to be a derivative of subsp. *bonariensis* and is thus far known only from cultivation. It might very possibly be a chromosomally homozygous derivative of the complex heterozygote *O. punae*, which in turn has been derived by the combination of various species of series *Renneria* with *O. indecora* subsp. *bonariensis*. The range of subsp. *bonariensis* extends to high enough elevations in the province of Salta so that this combination is possible. If this reasoning is correct, then *O. indecora* subsp. *boliviensis* provides an excellent demonstration of the way in which a genome can be altered when it is combined in a complex heterozygote. The F_1 generation derived by hybridizing *O. indecora* subsp. *bonariensis* with *O. punae* segregated, as might be expected, into two distinct classes of plants, one of which has the habit of *O. punae*, the other the more normal habit of *O. indecora*. This indicates that the normal habit of subsp. *bonariensis* is dominant over the nanism of subsp. *boliviensis*.

The absence of *O. indecora* subsp. *boliviensis* as a wild plant might be explained on the hypothesis that its genome can exist at high elevations only in combination with those derived from series *Renneria*. It should however be sought in the vicinity of La Paz, Bolivia.

20. **Oenothera affinis** Cambess. in St.-Hilaire, Fl. Bras. Mer. 2: 269. 1829.—FIGS. 58–59, 133, 180–181, 218.

O. berteriana Spach, Nouv. Ann. Mus. Hist. Nat. 4: 343. 1835. TYPE: Chile, Prov. Valparaíso, Quillota, *Bertero* (P, holotype, F and GH photographs; G, isotype); Ann. Sci. Nat. Bot., sér. 2, 4: 273. 1835.

O. chilensis Fischer & Meyer, Ind. Sem. Hort. Bot. Petrop. 45. 1835. LECTOTYPE: Cultivated in the Botanical Garden at Leningrad from seeds of the Botanical Garden at Paris, 1835 (LE).

O. macrosiphon Lehm. ex Otto, Hamburger Garten- Blumenzeitung 14: 439. 1858. Based on plants cultivated at Hamburg, the seeds received from Darmstadt as *O. villosa*; authentic material not seen. A contemporary specimen bearing this name, probably cultivated in Berlin, was in the K. Koch herbarium in Berlin until it was destroyed in World War II; a photograph and fragments are at POM.

O. mollissima L. var. *grandiflora* Micheli in Mart., Fl. Bras. 13(2): 178, *tab.* 38. 1875, pro parte.

Onothera polymorpha H. Lév. race *propinqua* (Spach) H. Lév. var. *berteriana* (Spach) H. Lév., Monogr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 324. 1909.

Raimannia berteriana (Spach) Sprague & Riley, Bull. Misc. Infor. 1921: 200. 1921.

Oenothera diplotricha Domin, Bibl. Bot. 22(89): 992. 1928. TYPE: Australia, South-Queensland, mixed forests at Logan River, on sand, 1910, *K. Domin III*. Not located.

O. mollissima sensu Munz, Physis 11: 282. 1933, pro parte; Amer. J. Bot. 22: 659. 1935, pro parte; Revista Univ. Chile 22. 1: 266. 1937, pro parte; Comun. Bot. Mus. Hist. Nat. Montevideo 1(10): 29. 1943, pro parte.

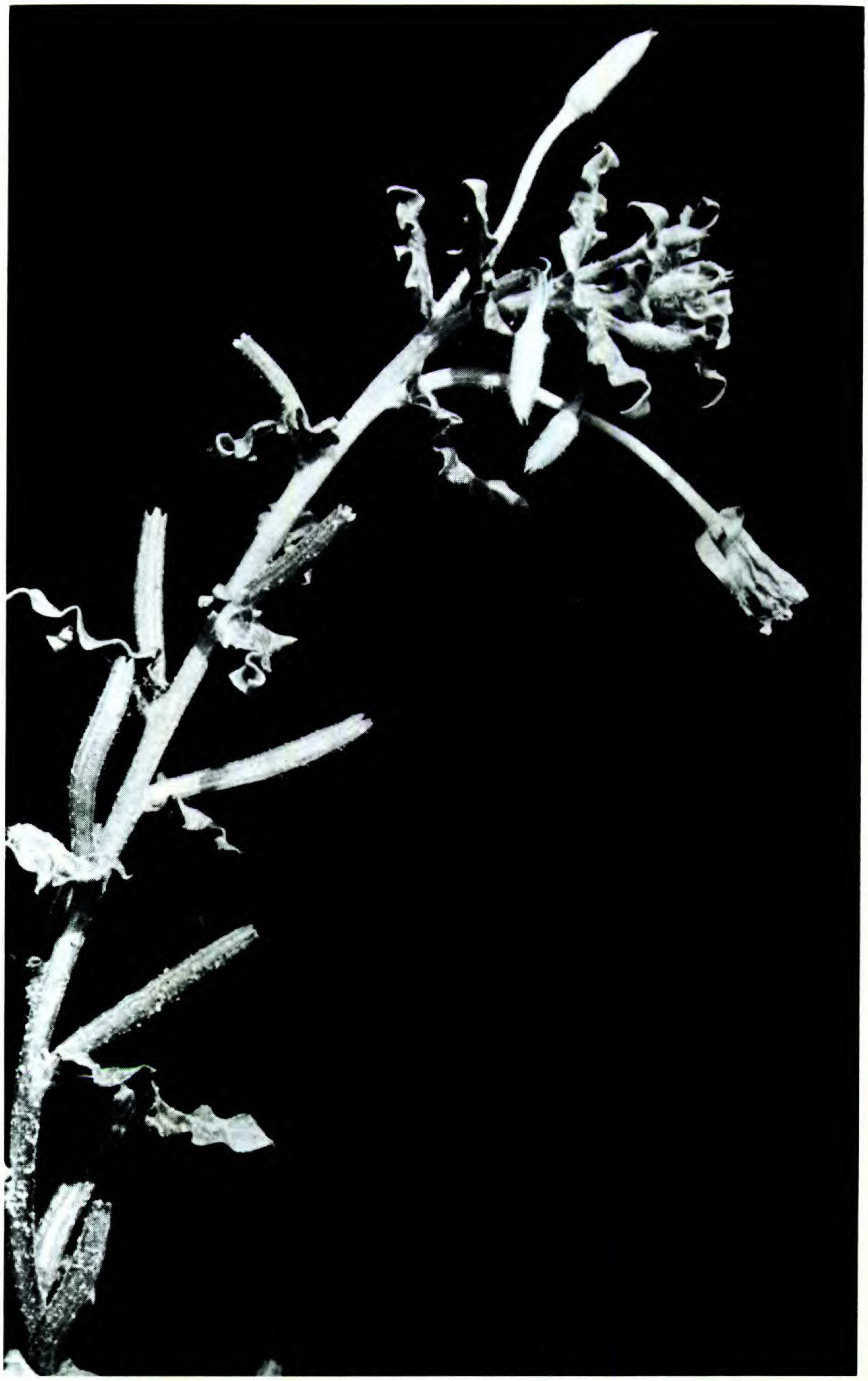


FIGURE 167. *Oenothera laciniata* subsp. *pubescens* (Peru, Junín, *Santarius 2190*).

O. mollissima "El Cuadrado" Cleland, Jap. J. Genet. 43: 332. 1968.
Oenothera affinis "longiflora Erlangen" Cleland, Jap. J. Genet. 43: 332. 1968.

Erect annual herb, not forming a rosette, unbranched or ± well branched throughout, 4–15 dm tall. Entire plant covered with soft hairs, densely to sparsely long-villous, the hairs erect, densely short-villous, and densely glandular-pubescent. Cauline leaves cultrate to narrowly lanceolate, acute, acute to rounded at the base, sessile, 5–15 cm long, 0.5–1.5 cm wide; bracts cultrate to narrowly lanceolate, acute, rounded to truncate at the base, sessile, longer than the capsules they subtend, (3–)4–9 cm long, 0.5–1.2 cm wide; leaves plane or weakly to evidently undulate at the margins, sparsely serrate with blunt teeth. Inflorescence branched. Floral tube 8–11(–13) cm long. Buds narrowly lanceolate to lanceolate in outline, green or yellowish green, often flushed with red, 2–3.5 cm long, 6–9 mm thick; apices of the sepals erect or divergent, 1.5–4 mm long. Petals very broadly obovate, (1.5–)2–4 cm long. Anthers 10–14 mm long. Filaments 15–20 mm long. Style long or short, the stigma held above the anthers at anthesis or surrounded by them, 9–13.5 cm long. Stigma lobes 5–10 mm long. Ovary 1.3–2 cm long. Capsule (2–)2.5–4(–5) cm long, 3–4 mm thick, thicker in the upper third, and with the 4 valves clearly separated at the apex. Seeds elliptic in outline, 1.5–2 mm long, 0.5–0.6 mm thick. Self-compatible; outcrossing or self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 14** or intermediate configurations at meiotic metaphase I). Flowering time: Brazil, Uruguay and eastern Argentina, September–May; central Argentina, October–April; Bolivia, Chile and northern Argentina, November–April.

Type: Brazil, Rio Grande do Sul, margins of woods near city of Rio Pardo, April (1816–1821), *Auguste de St.-Hilaire 2791-12* (P, holotype, F and GH photographs).

Distribution (Figs. 234, 244): In Brazil from Rio de Janeiro through Minas Geraís to Rio Grande do Sul. Apparently absent in the Atlantic departments of Uruguay, but frequent in the western, central, and southern departments of Ártigas, Salto, Paysandu, Río Negro, Soriano, Colonia, Flores, San José, Tacuarembo, Durazno, Florida, Canelones, and Montevideo. From northern Argentina the species extends to Tarija in Bolivia. It occurs throughout northern Argentina, where it ascends to an elevation of 2,500 m along the river valleys of the Andes, and in central and eastern Argentina. It occurs in the following provinces of Argentina: Jujuy, Salta, Tucumán, Catamarca, La Rioja, San Juan, Mendoza, Chaco, Formosa, Santiago del Estero, Santa Fé, Córdoba, San Luis, La Pampa, Misiones, Corrientes, Entre Ríos, and Buenos Aires. West of the Andes, the species occurs in Chile from the province of Atacama to Valparaíso.

Specimens examined from cultivated plants:

URUGUAY. MONTEVIDEO: Garden of the Facultad de Agronómia in Montevideo, *Santarius 193** (ring 6, 4 bivalents), *194-196*, *197**, *198-204* (DUSS; *193*, *197* also CTES, M, MO). Toledo, *Hecht 1964-95*** (CTES, DUSS, M, MO). Botanical Garden of the Facultad de Agronómia in Montevideo, *Rosengurtt B11256* (ring 6, 4 bivalents) (DUSS). FLORIDA: At the railroad about 1 km NE and 3 km SW of Mansavillagra, *Santarius 215*, *217*, *218* (ring 12, 1 bivalent), *220*, *222** (ring of 8, 3 bivalents), *223*, *224*, *225**, *226*, *228**, *229*, *230* (DUSS; *218*, *222*, *225*, *228* also CTES, M, MO). 3 km S of Arrayán at Ruta 7 near the Río Mansavillagra, *Santarius 242*** (DUSS). Florida, *Hecht 1964-1*** (DUSS, M, MO).

ARGENTINA. BUENOS AIRES: Garden of the Botanical Institution of the Facultad de Agronómia in Buenos Aires, *Santarius 259*, *261* (DUSS). Old gravel mine E of the road from Berisso to Los Talas, about 1 km SE of Villa Zula near La Plata, *Santarius 300**, *301**, *302*, *304*, *308-312*, *314**, *315-317*, *319*, *321*, *324-326*, *328* (DUSS; *300* also CTES, M; *300*, *310* also MO). Punta Lara near La Plata, *Gopel in 1961* (DUSS); *Hecht 1964-97* (DUSS). Botanical Garden of Buenos Aires, *Diers 19** (DUSS, M). Villa Ortuzor in Buenos Aires, *Hecht 1964-125** (CTES, DUSS, M, MO). ENTRE RÍOS: Gualeguaychi, Parque Unzue, *Burkart 23060*

(DUSS). Isla Almiron Chico near Concepción del Uruguay, *Burkart 23062* (DUSS). SANTA FÉ: Santa Fé, *Cleland 1965-426** (DUSS). CÓRDOBA: Córdoba, *Hecht 1964-90* (DUSS). El Cuadrado, *Cleland 1967-417*** (DUSS). SALTA: Dep. Cafayate, Tolombón near the border of Tucumán, 1,600 m, *Hunziker 21104* (CTES, DUSS, MO). JUJUY: In the bed of Río Xibi S of San Salvador de Jujuy, 1,250 m, *Santarius 1841**, 1842, 1843* (DUSS; *1841* also MO). In the bed of Río Grande N of San Salvador de Jujuy, 1,250 m, *Santarius 1849**, 1850** (DUSS; *1850* also CTES, M, MO). Road to Pucara, 1 km S of Tilcara, 2,450 m, *Santarius 1851*, 1852** (DUSS; *1851* also CTES, M, MO). Damp slope NE of Tilcara, about 150 m N of the cemetery, 2,500 m, *Santarius 1853*, 1854, 1855, 1857, 1860, 1863, 1867, 1869*, 1870-1872, 1877, 1878, 1881, 1882, 1884* (DUSS; *1869* also CTES, M; *1869, 1882* also MO). TUCUMÁN: Stony places, Río Salí, near the bridge of Ruta 9, E of San Miguel de Tucumán, 420 m, *Santarius 1672**, 1674, 1675** (DUSS; *1672, 1675* also M, MO). Bed of Río Lules, N and NW of Lules, 410 m, *Santarius 1679*, 1680* (ring of 6, ring of 4, 2 bivalents), *1682, 1685, 1687, 1693, 1695, 1697, 1699, 1702, 1709, 1711** (ring of 4, 5 bivalents) (DUSS; *1711* also CTES, M; *1680, 1697, 1711* also MO). Bed of Río Seco near bridge at Ruta 38, 450 m, *Santarius 1712* (ring of 8, 3 bivalents) (DUSS). Bed of Río Gastona near the bridge at Ruta 38, 450 m, *Santarius 1713* (ring of 6, 4 bivalents (DUSS, MO). Bed of Río Angostura, from Tafí del Valle to 5 km N, 2,000–2,250 m, *Santarius 1714*, 1718, 1722, 1724, 1727, 1730* (DUSS; *1714* also CTES, M; *1714, 1727* also MO). Bed of Río Angostura at km 24.5 of Ruta 307 near Tafí del Valle, 800 m, *Santarius 1788** (ring of 8, 3 bivalents), *1789–1791, 1794, 1799, 1800* (DUSS; *1788, 1799* also MO). At km 16.5–17, 570 m, *Santarius 1801* (ring of 8, 3 bivalents; ring of 8, ring of 4, 1 bivalent) (DUSS, MO). At km 11 in the bed of Río Totorilla, 430 m, *Santarius 1802* (ring of 4, 5 bivalents), *1803, 1804* (DUSS; *1802* also MO). Clavillo near Tucumán, *Cleland 1967-425** (CTES, DUSS, M, MO). LA RIOJA: Costadero to Mina, *Hecht 1964-120** (CTES, DUSS, M, MO, SP).

CHILE. COQUIMBO: Dry place at a road in a vineyard near Pisco del Elqui, *Stubbe in 1961* (ring of 12, 1 bivalent).

CULTIVATED. *O.* "*longiflora*" from the Botanical Garden in Erlangen, Germany, received 1962* (CTES, DUSS, M, MO).

Representative specimens examined:

BRAZIL. MINAS GERAÍS: Caldas, *Hoehne 2799* (POM, SP). Between Carandaí and Crespo, *Duarte 524* (BR). Morro de Cruzeiro near Ouro Preto, *Emygdis 2881* (R). RIO DE JANEIRO: Villa Theresa, *Glaziou 8344* (G, K, LY, P). SÃO PAULO: Pinheiros, *Usteri 11896* (SP). São Paulo, *Hoehne 11670* (POM). Ipanema, *Galvão in 1884* (R). Belémsinho, *Porto 11670* (SP). PARANÁ: Oure Fine near Bocayúva do Sul, *Hatschbach 963* (HB). Rio Jangada near Palmas, *Hatschbach 3493* (RSA). Serro Azul, *Rambo 11199* (SP). Rio Cavernoso near Guarapuava, *Pereira 7696* (HB). Rio Perdido near Laranjeiras do Sul, *Hatschbach 19855* (UC). SANTA CATARINA: Garopaba, *Klein & Bresolin 8850* (HBR). Valley of Rio Pelotas, *Pabst & Pereira 6224* (HB). Lajes, Morro do Pinheiro Seco, 1,000 m, *Reitz 6601* (HBR). Itapiranga, 200 m, *Klein 5200* (HBR, RSA). Banks of Rio Uruguai near Mondaí, *Smith & Reitz 9728* (HBR, R, RSA, US). Ubatuba, *Hans 311* (R). RIO GRANDE DO SUL: Banks of Rio Ibira Puitan near Alegrete, *Palacios & Cuezzo 1837* (LIL). Rio Pardo, *Jörgens 16* (B). Serro Largo, *Sehnem 3549* (SI). Between S. Angelo and Guarani das Missões, *Santos 2727* (R).

URUGUAY. ÁRTIGAS: Arroyo Tres Cruces Grande, *Praderi 2540* (LIL). SALTO: San Antonio, *Osten 5423* (SI). PAYSANDÚ: M. Cassioni, *Puerto 8303* (MVFA). SORIANO: Fray Bentos, *Fruchard in 1877* (P, RSA, US). Sta. Elena, *Rosengurtt PE-4386* (GH, LIL, MO, SP). COLONIA: Colonia Valdense, *Dubugnon 77* (G). TACUAREMBO: Valle Edén, *Arrillaga 1733* (MVFA). DURAZNO: Between Río Negro and Est. km 329, *Ziliani 10549* (MVFA). FLORIDA: Mansavillagra, *Rosengurtt B791* (GH, POM). FLORES: Río Yi, *Rosengurtt B564* (POM). SAN JOSÉ: Barra Santa Lucia, *Osten 4551* (G). Arazati, *Rosengurtt 1696* (POM). CANELONES: Arroyo de Saúce, *Bartlett 20963* (GH, MICH, NY, P, UC, US). MONTEVIDEO: Sta. Lucía, *Fruchard in 1972* (P). Colón, *Osten 3714* (G). Montevideo, *Isabelle in 1838* (W).

PARAGUAY. Alto Paraná, *Montes 9929* (LIL).

BOLIVIA. TARIJA: Tarija, *Fries 1125* (S); *Zelada 41* (LIL); 2,000 m, *Fiebrig 2435* (BM, G, K). Padcaya, 2,100 m, *Fiebrig 2545* (BM, G, LY).

ARGENTINA. JUJUY: Yala, 1,600 m, *Arnow 3747* (MO). Tilcara, ca. 2,400 m, *Balls 5955b* (F, K, UC, US); *Meyer in 1940* (F, GH, LIL-33737, NY, SI). Quebrada de la Huerta near Huacalera, 2,700 m, *Cabrera 12041* (BAB). El Fuerte near Sta. Báebara, *Cabrera 17273* (BAA, LP). SALTA: La Candelaria, 1,200 m, *Schreiter 9436* (GH, LIL). Pampa Grande, *Hohnberg 6906* (BAB). El Morenillo near Rosario de la Frontera, 690 m, *Carbone 10088* (LIL). Victoria, *Meyer 5040* (LIL, UC). Cachí, *Garolera-Romero in 1947* (LIL, RSA).

Tolombón near Cafayate, 1,600 m, *Hunziker 21104* (CORD, MO); *Hayward 002066* (LIL). TUCUMÁN: Río Churqui, *Lillo 7512* (LIL, US). Río Salí near Tucumán, 600 m, *Venturi 999* (GH, LIL, POM, SI, US). Río Cochuna near Chicligasta, 915 m, *Munz 15476* (GH, NY, POM, US). Tafí del Valle, *Araque & Barkley 19Ar161* (F, LIL). Cerro Muñoz near Tafí, 2,500 m, *Lillo 1241* (LIL). Río Lules, 760 m, *Mexia 04354* (GH, MO, UC). Río Tipamayo near Trancas, *Venturi 4218* (GH, LIL, NY, POM, US). S. Pedro de Colalao near Trancas, *Krapovickas & Cristóbal 15339* (CTES). Cerro del Campo near Burroyacú, 2,000 m, *Venturi 7748* (K). CATAMARCA: Andalgala, *Jörgensen 1054* (BAB), *1055* (GH, LIL, MO, POM, SI); *Rodríguez 344* (GH, LIL, S, UC). Río Pomancillo, *Spegazzini 29563* (BAB). San Antonio near Padín, *de Ance in 1957* (SI). El Portezuelo, *Bartlett 19613* (MICH, US). Yacutula near Belén, *Schickendandz 131* (CORD, GOET). Barranca Larga near Belén, 2,400 m, *Schreiter 10248* (LIL). Near Capayán, *Risso 556, 565, 626, 770* (LIL). Sta. María, Cerillos, 3,000 m, *Peirano in 1933* (LIL). Sierra de Ambato, between Mutquin and Pomán near Colana, 1,650 m, *Hunziker et al. 18406* (CORD, MO). LA RIOJA: Sierra Famatima, Alto Carrizal, *Calderon 1044* (BAA). La Hoyada, 2,500 m, *Kurtz 15041* (CORD, MO). Guanchin Viejo, *Castellanos 28-284* (BA, POM). Santa Cruz, *Toscani 32* (BAB). Campanas, 1,850 m, *Rojas Paz in 1942* (GH, LIL, NY). Rodeo de Las Vacas, 3,000–4,000 m, *Flossdorf 40* (SI). Dep. Capital, El Cantadero, 1,200 m, *Meyer 3939* (GH, LIL, UC). Sierra de Velazco, El Cantadero, 2,300 m, *Hunziker 5270* (CORD, SI). Yacuchi, *Kurtz 15414* (MO). Punta de Agua near Gral. Sarmiento, 2,600 m, *Hunziker 2083* (CORD, POM). Los Molles near Lamadrid, 2,700 m, *Krapovickas & Hunziker 5530* (BAB, CORD). SAN JUAN: Between Rodeo and Colanguil near Iglesias, *Castellanos 15495* (US). Dep. Calingasta, Las Lumbreras, 2,000 m, *Spegazzini 656* (BAB). Río Calingasta near Calingasta, *Zarchini 150* (CTES). Quebrada de Huachi near Jachal, 1,500 m, *Rodrigo 2993* (LP). Chimbas near Desamparados, *Cuezzo 1266* (LIL, RSA). Valle Fertil, *Hunziker 16686* (CORD). Villa Krause near Pocitos, *Cuezzo 2175* (LIL). La Bebida near Rivadavia, *Cuezzo 1433* (LIL). MENDOZA: *Philippi 614a* (SGO). Junín, *Ruiz Leal 7033* (Leal, LIL). FORMOSA: *Hicken* (SI-4851). Pirané, *Morel 638* (LIL). Uriburú at Río Bermejo, *Kermes 68660* (BAB). CHACO: Las Palmas, *Jörgensen 2488* (GH, LIL, SI, US). Resistencia, *Meyer 3212* (LIL, POM). Fontana near Resistencia, *Meyer 456* (LIL, SI). Colonia Benítez, *Stuckert 19511* (CORD, G); *Schulz 501* (POM). Fortín Anguilar, *Hossens in 1917* (CORD). SANTIAGO DEL ESTERO: Dep. Rivadavia, between Selva and Palo Negro at Ruta 34, 100 m, *Hunziker 17776* (CORD, MO). SANTA FE: Mocoví, *Venturi 275* (SI); *Quarin 1145* (CTES). Monje, *Pedelaborde in 1940* (LIL, SI). At Ruta 9 across the Río Caracaraná near Iriondo, *Hunziker 13702* (CORD, MO). Reconquista, *Venturi 275* (LIL, POM). Las Colonias near Pilar, *Terribile 474* (LIL). Aurelia near Castellanos, *Terribile 490* (LIL). CÓRDOBA: Banks of Río Primero near Ojo de Agua, *Hunziker 11920* (CORD, MO). Gral. Paz, *Stuckert 3730* (CORD, G, MO). Sierra San Ignacio near Quintas, *Stuckert 18586* (CORD, G). Dique Los Molinos near Calamuchita, *Krapovickas & Cristóbal 14714* (CTES). Río Tercero, *Burkart 10369* (MO, SI). Near Santa María, *Krapovickas 6514* (BAB, CORD, LIL). Capilla del Monte, *Nicora in 1941* (SI-17600). Totoral, *Domínguez 106* (POM). La Carlota near Juárez Celman, *Hossens 385* (CORD). Córdoba, *Lorentz 308* (CORD, GOET); *Hieronymus in 1878* (FR); *Lossen 128* (G, LE, M, SI, Z). Ascochinga, *Giardelli 845* (SI). Las Compuertas at Río Segundo, *Sublis 1171* (CORD, MO). Sierra Chica, between Pan de Azúcar and Villa Allende, *Hunziker 11932* (RSA). Cruz del Eje, *Meyer 13042* (LIL). San Javier, *Castellanos 10734* (RSA); *Fabris & Moreau 6791* (BAB, LP). Capilla del Monte, *Hossens 427* (CORD). Copina, *Hieronymus 333* (P). Los Cocos near Punilla, *De la Sota 3278* (LIL). SAN LUIS: Sierra de Comechingones, El Rincón, *Hunziker 11852* (CORD, MO). Piedra Blanca near Merlo, 1,000 m, *Digilio-Grassi 2066* (LIL, RSA). Trapiche, *Gez 31-278* (POM). Quebrada de los Bueyes, *Galander in 1882* (CORD). LA PAMPA: Between Chamaico and Casimiro Gomez near Rancul, *Cabrera & Sagastegui 19406* (LP). MISIONES: Corpus near San Ignacio, *Schwarz 3411* (LIL, S). Gob. Roca near San Ignacio, *Schwarz 6413* (LIL). San Ignacio, *Quiroga in 1913* (POM). San Pedro, *Bertoni 2101* (LIL). Victoria at Ruta 12 near Iguazú, 170 m, *Schmidt 2743* (LIL). Bonpland near Posadas, *Lilliesköld* (F, S). Garupá near Cainguas, *Bertoni 4660* (LIL). Santa Ana, *Rodríguez 109* (GH, LIL, SI, UC). Candelaria, Ruta 105, *Mroginski 430* (CTES, MO). CORRIENTES: Mercedes, *Rodrigo 711* (LP, NY). Est. "La Pastoril," at Río Paraná near Lavalle, *Pedersen 3858* (BR, C, G, UC, US). Monte Caseros, *Nicora 5748* (BAA, CTES). Paso de los Libres, *Ibarrola 2002* (LIL, NY, S); *Schinini 7698* (CTES, MO). Santo Tomé, *Ibarrola 1233* (LIL, NY). Curuzú Cuatiá, *Spegazzini 154* (BAB). Bella Vista, *Schinini 6565* (CTES, MO). ENTRE RÍOS: Concepción del Uruguay, *Lorentz 628* (BREM, COI, CORD, F, FR, G, HBG, K, L, LE, LY, M, UPS, W, Z), *12* (GOET). Arroyo

Martínez, *Boelcke 907* (BAA). Paraná, *Frommel & Lefebre in 1888* (P). Paracao near Paraná, *Burkart 23762* (MO). Calera Barquin near Colón, *Pozzi 27-1572* (POM). La Paz, *Burkart 21312* (SI). Federación, *Meyer 11130* (LIL). Diamante, *Burkart 22243* (MO, RSA). Isla Almiron Chico, *Burkart 23062* (MO). Gualeguaychú, *Burkart 23060* (MO). BUENOS AIRES: Delta, Río Carabelas near Tiburón, *Scala in 1925* (NY). Est. Las Palmas near Zárate at Río Paraná, *Boelcke 13166* (BAA, MO). Hudson near La Plata, *Eyerdam & Beedle 23156* (G, GH, K, MO, UC). Pereyra near La Plata, *Cabrera 7607* (LP). Palermo, *Munz 15460* (NY, POM, US). Los Talas near Berisso, *Boffa 171* (F, LIL, S). Atucha near Gral. Uriburu, *Krapovickas 3290* (BAB, LIL). *San Isidro, Parodi 8565* (GH). Martín Garcia, *Boelcke 5034* (SI). Otamendi, *Fabris 4995* (LP). Pergamino, *Boelcke 2215* (BAA). Punta Lara, *Dawson 854* (F, GH, LP, NY); *Rodríguez 520* (S, SI).

CHILE. ATACAMBA: Valley of Río Transito, La Pampa near Vallenar, *Johnston 5860* (GH, K, POM). Higuerita near San Félix, 1,300 m, *Ricardi 3867* (CONC). COQUIMBO: *Gay in 1838* (P). Rivadavia, 800 m, *Werdermann 175* (BM, F, G, GH, HBG, LIL, MO, SI, UC, Z). Rapelcillo near Ovalle, 800 m, *Jiles 1958* (CONC). Between Pauhuano and Elqui, *Pfister 6498* (CONC). Tunga near Illapel, *Landbeck in 1962* (SGO). ACONCAGUA: Los Andes, 1,100 m, *Behn 22802* (CONC); *Scott Elliot 436* (BM); *Philippi in 1885* (HBG, SGO). San Felipe, *Claude-Joseph 2508* (US). Chupaja, *Jelinek* (W). Near Papudo, *Zöllner 5168* (L). VALPARAÍSO: *Petre in 1818* (S), *in 1827* (W). Laguna Verde, 100–150 m, *Eyerdam et al. 10040* (F, NY, UC, US). Concón, *Poeppig 121* (BM). Limache, *A.J.H. in 1927* (M). Quillota, *Maximowitsch 133* (LE). SANTIAGO: *Philippi 886* (P, LE). Salto de Conchalí, *Philippi 614b* (SGO); *Marques in 1878* (HBG). Cordillera de Santiago, *Germain in 1856–57* (FR, G, K, W). Cerro de Renca, *Gusinde 643* (W). ISLA JUÁN FERNANDEZ: Cumberland bay, valley of Lord Anson, *Bock in 1931* (SGO). Province unknown: Aeuleo, *Bertero 464, 1185* pro parte (BM, W). Farillar, *Volckmann 28* (SGO).

Specimens from outside of South America (naturalized):

SCOTLAND. Selkirk, 1965, *Webster 10169* (BM, E).

SPAIN. Railway station of San Sebastian, *Guillon in 1877* (MPU). Oña, *Arraiano in 1881* (COI).

PORTUGAL. ESTREMADURA: Sandy places near Lagoa Obidos, *Daveau in 1882* (BM, COI, LISU). Samouco, 1882, *Coutinho 1273* (LISU). Barreiro, *da Cunha in 1888* (LISE, LISU). Trafaria, *Daveau 3093* (BM, LISU); *Jonge in 1912* (BAS). Moita, *da Cunha in 1889, in 1891* (LISE), *in 1890* (LISU). Brejo do Cobre, *Santoz in 1905* (LISU). Caldas da Rainha, *in 1890* (COI); 1938, *Rothmaler 14098* (LISE). Praia das Macăs near Sintra, 1950, *Rainha 1974* (LISE, UPS). S. Marinho do Pôrto, 1961, *Rainha 5060* (LISE). ALGARCE: Faro, *Guimaraes in 1880, in 1882* (COI). Tavira, *Daveau in 1890* (LISU).

PAKISTAN. West Himalaya, Hazara, *Duthie in 1899* (K); 1963, *Nasir & Siddiqi 1821* (RAW).

INDIA. Punjab, Abbotabad, 1922, *Drummond 20096* (K). Punjab, Manikeru village in valley Parshatti near Kulu, 1934, *Parkinson 3923* (K). Prov. Madhya Pradesh, Balakot, 1959, *Jafri & Ali 3264* (K).

AUSTRALIA. QUEENSLAND: Currumbiu Beach S of Brisbane, *Longman in 1961* (K). Moreton near Southport, 1936, *Pedley 79* (K). Bubya Mountains, 1944, *Clemens 43807* (LIL). South Pine River near Moreton, 1964, *Henderson H97* (K). NEW SOUTH WALES: Bellbrook, *Lengoth in 1891* (MEL-58126). Conjola, *McHeron in 1899* (NSW-135171). Rockdale, *Campfield in 1902* (NSW-135174). Bega, *Tielkens in 1906* (NSW-135172). Tweed Heads, *Cheel in 1916* (NSW-135176). Sussex, *Maiden in 1917* (NSW-135170). Urunga, 1917, *Lawrence 8132-17* (NSW). Warialda, *Gillings in 1920* (NSW-135167). Wondabyne to Woy Woy, *Blakely in 1922* (NSW-135173). Bomaderry, *Rodway in 1936* (NSW-135175). Moura, *Rodway in 1936* (K, NSW-135169). Gearge's Creek, upper Macleay River, *Danis in 1941* (NSW-135180). Grafton, *O'Grady in 1951* (NSW-135178). Kyogle Distr., *Vane in 1958* (NSW-135177). At Manning River near Wingham, 1964, *Salasoo 2820* (NSW). Merriwa, 1970, *Raven et al. 25866* (K, MO, NSW). Bylong, ca. 30 mi NE Mudgee, 800 m, 1970, *Raven et al. 25869* (MO, NSW, PERTH). N Milton on Princess Highway, 1970, *Raven et al. 25894* (K, MO, NSW). Brogo, 12 km N Bega, 1970, *Briggs 3970* (K). 1 mi W Tabulam, 1971, *Salasoo 4609* (NSW). SOUTH AUSTRALIA: Encounter Bay near Port Elliot, 1895, *H. 392* (MEL). WEST AUSTRALIA: Bunbury, *Wickens in 1910* (BM). 25 mi E of Albany, *Elder in 1932* (NSW). Mi Lawley, *Lyon in 1966* (PERTH).

HAWAII. Parker Ranch, 1929, *Carter & Brown 182* (K). Mauna Kea, near pit where David Douglas was murdered, 1949, *Degener et al. 20344* (K, MO).

SOUTH AFRICA. CAPE: At P.P. Rust, 1905, *Rogers 4117* (PRE). Paarl, 1916, *Smith 2667* (K), 1926, *2667* (K, PRE). Roadside near Faure, Distr. Stellenbosch, 1968, *Parker 4390* (K). TRANSVAAL: Nylstroom, 1902, *de Jongh 6529* (PRE). Distr. Pretoria, Scheerport, 1906, *Leendertz 8295* (PRE). Rutzenburg, 1910, *Leendertz 9568* (PRE). Transvaal, *Davy 1248* (PRE). NATAL: Distr. Durban, Isipingo, 1961, *Ward 3764* (PRE). Distr. Umzinto, Shelley Beach, 1967, *Strey 7281* (K, M, MO, PRE). LESOTHO: Morija, 1918, *Dieterlen 1352* (P, PRE).

Old specimens from plants cultivated in gardens:

Munich, Germany, Herb. *Zuccarini in 1835* (M; as *O. undulata*). Paris, *in 1835* (P; as *O. chilensis*). Jardin du Luxembourg, *in 1837* (K; as *O. chilensis*). Vienna, Austria, *in 1849*, (W as *O. villosa*).

Oenothera affinis reported in literature from outside of South America:

PORTUGAL: Raven (1968).

SOUTH AFRICA: Ross (1972: 262).

AUSTRALIA: Bailey (1900: 681; 1913: 215) (as *O. longiflora*); Black (1909: 63; 1926: 427 (as *O. longiflora*); 1952: 638); Beadle et al. (1962: 173).

More or less clavate capsules with the valves clearly separate at the apex, a long floral tube, and a dense vestiture of soft pubescence are the most obvious characteristics of *O. affinis*. In comparison with *O. odorata*, the variation is limited. Relatively leafy plants with broad leaves occur throughout the range, especially in the east, but less densely leafy ones in which the leaves are relatively narrow occur only in the northern part of the area of distribution—Bolivia and the provinces of Argentina along the eastern flanks of the Andes.

Just as in *O. odorata*, there are included in *O. affinis* complex heterozygotes which are indistinguishable from the homozygotes of the same species. Both sorts of plants occur in the same populations in *O. affinis*, together with all possible intermediates between 7 pairs and a ring of 14. For example, plants from the vicinity of Tucumán had the following configurations: *Santarius 1672*, ring of 14; *1675*, 7 pairs; *1679*, 7 pairs; *1680*, ring of 6, ring of 4, 2 pairs; *1711*, 7 pairs, another with ring of 4, 5 pairs; *1712*, ring of 8, 3 pairs; *1713*, ring of 6, 4 pairs; *1714*, 7 pairs; *1788*, 7 pairs, another with ring of 4, 5 pairs; *1801*, ring of 8, 3 pairs; ring of 8, ring of 4, 1 pair; *1802*, ring of 4, 5 pairs; *Cleland 425*, 7 pairs. See the general remarks in the introduction on p. 437.

21. **Oenothera mollissima** L., Sp. Pl. 346. 1753.—FIGS. 60–62, 134, 182, 219.

Onagra mollissima (L.) Moench, Meth. Pl. 1: 675. 1794.

Oenothera mollissima L. var. *villosa* Sprengel, Pl. Min. Cog. Pug. Prim. 2: 60. 1815. TYPE: not seen.

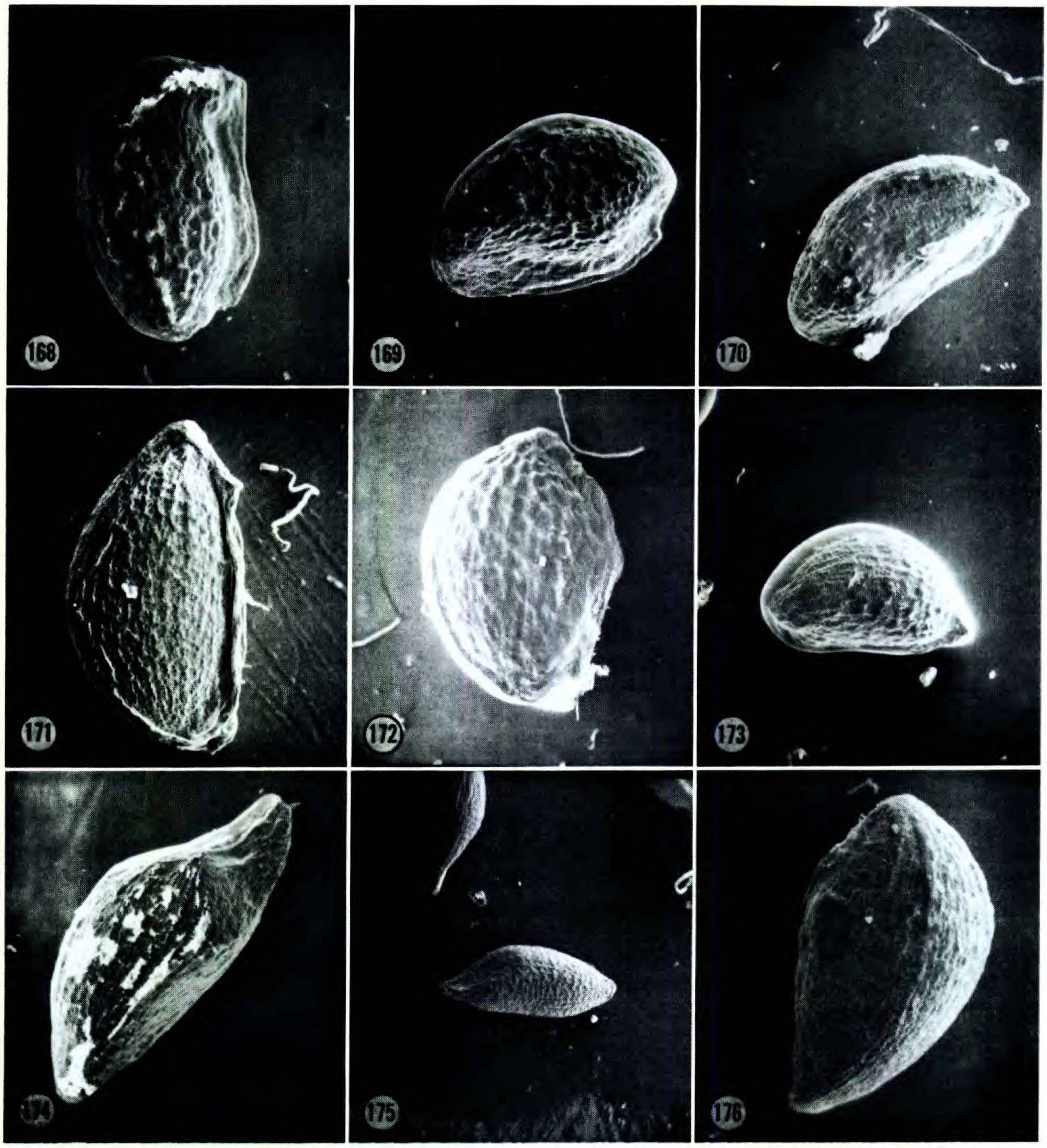
O. holosericea Tausch, Flora 22: 558. 1839. LECTOTYPE: Cultivated in botanical garden, 1836, *J. F. Tausch* (PRC, POM photograph); Munz, Amer. J. Bot. 22: 661. 1935.

Onothera polymorpha H. Lév. race *mollissima* (L.) H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909.

Oenothera mollissima L. var. *genuina* Hassler, Bull. Soc. Bot. Genève, sér. 2, 5: 274. 1913.

Raimannia mollissima (L.) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.

Annual herb, not forming a rosette, the main stem erect or rising obliquely, unbranched or ± well branched, with the side branches arising at right angles or ± obliquely, 3–10 dm tall. Plants densely or very densely and softly long- and short-villous and densely glandular-pubescent. Lower cauline leaves very narrowly elliptic to narrowly elliptic, acute, narrowly cuneate to acute at the base, sessile, 4–7 cm long, 0.5–1.2 cm wide; upper cauline leaves and bracts narrowly oblong to lanceolate, acute, rounded to truncate at the base, sessile; bracts 2–4 cm long, 0.5–1 cm wide, longer than the capsules they subtend, as-



FIGURES 168–176. Scanning electron micrographs of seeds of taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—168. *O. peruana* (Peru, Arequipa, *Santarius 2106*).—169. *O. versicolor* (Peru, Junín, *Santarius 2163*).—170. *O. lasiocarpa* (Argentina, Tucumán, *Diers in 1959*).—171. *O. santarii* (Argentina, Mendoza, *Santarius 1430*).—172. *O. longituba* (Argentina, Tucumán, *Santarius 1736*).—173. *O. scabra* (Bolivia, Cochabamba, *Santarius 2003*).—174. *O. mendocinensis* (Argentina, Buenos Aires, *Santarius 415*).—175. *O. odorata* (Argentina, Río Negro, *Santarius 800*).—176. *O. ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul, *Hackbart in 1966*).

cending and overlapping towards the apex of the stem; leaves plane to strongly undulate along the margins, distantly serrate with blunt teeth. Inflorescence branched. Floral tube (1.5–)2–5 cm long. Buds oblong to lanceolate in outline, green or yellowish green, often red-striped at the junction of the sepals with the floral tube, 0.8–1.5 cm long, 3.5–6 mm thick; apices of the sepals erect, 1–2 mm long. Petals obovate to very broadly obovate, often broadly elliptic, 0.8–2 cm long. Anthers 4–8 mm long. Filaments 7–12 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.5–6 cm long. Stigma lobes 3–5 mm long. Ovary 1–1.3 cm long. Capsule 2.5–3.5 cm long, 3–4 mm thick, often slightly enlarged in upper third. Seeds elliptic in outline, 1.5–2 mm long, 0.7–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 12 and 1 bivalent** at meiotic metaphase I). Flowering time: October–July.

Lectotype: Grown in Cliffort's Garden in Hartekamp, Netherlands, 1735–1737, _C. Linnaeus_ (BM; GH and POM photographs). Said to be from the fields of Buenos Aires, Argentina. Linnaeus's diagnosis in the _Species Plantarum_ is taken directly from _Viridiarum Cliffortianum_ (1737) so the species must be typified by material he had available at that time.

Distribution (Fig. 232): Exclusively in the eastern portion of the range of series _Allochroa_. In Brazil it occurs in the two southernmost states, Santa Catarina and Rio Grande do Sul; in Uruguay, only in the coastal departments of Rocha, Maldonado, Montevideo, Florida, Canelones, San José, and Colonia; in Argentina, it is found in the provinces of Misiones, Corrientes, Entre Ríos, and Buenos Aires.

Specimens examined from cultivated plants:

URUGUAY. MALDONADO: Sandy place in E part of Piriapolis, _Santarius 117*, 118–122, 123*, 124–129_ (DUSS; _117, 123_ also CTES, M; _117, 118, 123, 128_ also MO). Sandy places in S part of Piriapolis, _Santarius 130*, 131–134, 135*, 136–138, 139*, 140–143, 144*, 145, 146, 148, 149, 151_ (DUSS; 130, 144, 151 also CTES; _130, 144,_ also M; _130, 134, 139, 144, 151_ also MO). Dunes E of Piriapolis, _Santarius 157*, 158–173_ (DUSS; _157_ also M; _157, 166_ also MO). Dunes in the W district La Pastora of Punta del Este, _Santarius 174*, 175–185, 186*, 187–191, 192*_ (DUSS; _174, 186, 192_ also CTES, M, MO). Dunes on the coast near Piriapolis, _Krapovickas & Cristobal 11147*_ (DUSS, MO). MONTEVIDEO: Dunes near Carrasco and Miramar, _Santarius 2*, 3–8, 10, 13*, 14, 16, 19–22, 23*, 24*, 25, 26, 29–31_ (DUSS; 2, 13, 23, 24 also CTES; _2, 3, 13, 23, 24_ also M, MO). Dunes and pine forest in the Parque F. D. Roosevelt, 3–4 km E of Carrasco, _Santarius 32*, 33–35, 36*, 37, 38, 39*, 40, 41, 42*, 43*, 44–47_ (DUSS; _39, 42, 47_ also CTES, M; _32, 36, 39, 42, 47_ also MO). Carrasco, _Hecht 1964-61*_ (DUSS). Montevideo, _Hecht 1964-87*_ (DUSS). Toledo, _Hecht 1964-88*_ (DUSS). CANELONES: Canelones, _Hecht 1964-25*_ (DUSS, MO). COLONIA: Sandy place, port of Juan L. Lacaze, _Santarius 48*, 49, 50*, 51–53_ (DUSS; _50_ also CTES, M; _48, 50_ also MO). At roads in W part of Juan L. Lacaze, _Santarius 67*_ (DUSS). Sandy place in the N part of Juan L. Lacaze, _Santarius 80, 92*, 93–98, 99*, 100, 101*_ (DUSS; _99, 101_ also CTES, M; _94, 99, 101_ also MO). Dunes NW of Juan L. Lacaze, _Santarius 102*, 103–108_ (DUSS; _102_ also MO). FLORIDA: At the railroad 1–3 km NE and SW of Mansavillagra, _Santarius 214**, 221*_ (CTES, DUSS, M, MO; 214 also SP).

ARGENTINA. CORRIENTES: At Ruta 40 8 km N of Santo Tomé, _Krapovickas & Cristóbal 16406*_ (DUSS, MO). BUENOS AIRES: Garden of the Botanical Institution of the Faculdad de Agronómia in Buenos Aires, _Santarius 256*, 263, 264, 265*, 266, 267_ (DUSS; _256, 265_ also CTES, M; _256, 264, 265_ also MO). Botanical Garden of Buenos Aires, _Göpel in 1961*_ (CTES, DUSS, M, MO). Villa Gesell in General Madariaga, _Burkart in 1962*_ (CTES, DUSS, M, MO).

CULTIVATED: From the main school garden in Frankfurt, Germany, received 1959*, source unknown (CTES, DUSS, M, MO). From the Botanical Garden in Erlangen, received 1960* (CTES, DUSS, M, MO).

Additional specimens examined:

BRAZIL. SANTA CATARINA: Campo de Massiambu near Palhoça, 5 m, _Reitz 4880_ (HBR), _Reitz & Klein 1222_ (HBR). RIO GRANDE DO SUL: Fazenda Bernardo Velho near Bom Jesus, 1,000 m, _Rambo 34863_ (S); between Capão da Canoa and Osório, _Nelson in 1970_ (BR); Torres, _Rambo 56194, 54791_ (HBR), _Burkart 25105_ (SI); city of Rio Grande, _Malme 244, 244a, 270_ (S); S. Leopoldo, _Rambo 1283_ (LIL); Ilha dos Marinheiros, _Schwacke_ 2599 (R); Praia de Tramandahy, _Vidal in 1913_ (R).

Uruguay. COLONIA: *N.N. 28* (BAA); Riachuelo, *Cabrera 3340* (NY); Arroyo de Pintos near Puerto Platero, *Bartlett 20771* (GH, MICH, NY, UC); Playa Fomento, *Puerto 1041* (MVFA). SAN JOSÉ: Barra de Sta. Lucía, *Herter 168e* (B); Eifler, *Herter 168g* (US, Z); Playa Pascual, *Arrillaga 742* (MVFA). CANELONES: Toledo, *Herter 168f* (B, GOET, L, SP, Z); Balneario San Luis, *Zorrón 1718* (MVFA, P); Camelon Chico, *Berro 5635* (MVFA); Atlantida, *Osten 21655* (BREM, F, GOET), *Barattini in 1940* (MO); Ruta Interbalneario at km 275, *Lema 6750* (MVFA); Arroyo Sarandi, *Izaguirre 149* (MVFA); El Pinar, *Arrillaga 435* (MVFA); Las Piedras, *Fruchard in 1869* (P); dunes near Floreta, *Steer in 1923* (HBG). MONTEVIDEO: *Rosa-Mato 1509* (LIL), *Isabelle in 1838* (W), *Chabataroff in 1939* (GH), *Gibert 86b, 340, 342* (K), *Gibert 1175* (W), *Gaudichaud in 1839* (G); Carrasco, *Munz 15441* (POM), *15449* (GH, POM), *Felippone 2078* (SI), *Kuhlmann in 1948* (BR); Buceo, *Fruchard in 1875* (P); Playas Blancas, *Fruchard in 1874* (P); Pocitos, *Fruchard in 1876* (NY, RSA, S, SI, US), *Herter 168a* (LE, M, Z), *168b* (G), *76266* (S); Cerro, *Herter 168* (GH, LIL, MO, SI, UC); Punta Gorda, *Rosengurtt B4331* (LIL, MO, MVFA, SP, US); Plata, *Courbon in 1856* (RB); Malvín, *Felippone 2325* (SI), *Herter 168d* (F, HBG, NY). ROCHA: La Paloma, *Descole 174* (LIL); Santa Teresa, *Léon 338* (BAA); La Pedrera, *Rosengurtt 9944a, 9944b* (MVFA), *Hossens 18* (CORD); Cabo Polonio, *Hossens 113* (CORD). MALDONADO: *Berro 3667* (MVFA), *Lourteig 168* (LIL), *Costa 7199* (MVFA); Punta del Este, *Descole 74* (F, GH, LIL, NY); dunes near Solis, *Osten 22389* (S); Cerro Ingles, *Osten 5300* (CORD, SI); Cerro San Antonio near Piriapolis, *Pabst 5496* (HB); San Rafael, *Descole 27* (LIL); Punta Ballenas, *Krapovickas & Cristóbal 12691* (CTES). Department unknown: Road to Lanañaga, *Felippone 2642* (SI).

Argentina. MISIONES: Santa Ana near Candelaria, *Montes 1517* (RSA); road to La Plantadora near San Ignacio, *Scala 258* (LIL); El Dorado near Iguazú, *Schwindt 2231* (LIL); Tapiorny near Cainguas, 215 m, *Schwindt 813* (LIL). ENTRE RÍOS: Concepción del Uruguay, *Lorentz 35* (POM). BUENOS AIRES: *Andersson in 1852* (S), *Rohl 4497* (W); Villa Gesell near Gral. Madariaga, *Boelcke 54* (BAA, MO), *Burkart 22376* (SI); dunes near Pinamar, *Cabrera 10099* (LP), *10674* (LIL, LP); Dock Sur, *Molfino 785* (POM); Isla Paulino, *Cabrera 7384* (F); Punta Lara, *Molfino 247* (POM), *Pujales 54* (LIL); Agua de Oro near Colón, *Dawson 1100* (LP); isle of Martín Garcia, *Moreau in 1933* (RSA); *N.N. in 1949* (SI 26721), *Palacios 35* (LIL); Necochea, *Rodriguez 848* (LIL, S); Jáuregui near Luján, *Burkart 18493* (SI); Juancho near Gral. Madariaga, *Pastore in 1936* (SI 26720), *Cabrera 2715* (LP, NY); San Clemente, *Cabrera 4262, 4271* (LP), *Cabrera 4921* (NY), *Krapovickas 132, 2874* (RSA); *Lourteig 465* (GH, LIL), *Krapovickas 1924* (LIL), *Vervoorst 5208* (BAB); between San Clemente del Tuyú and Mar de Ajó, *Tortosa & Medán 11058* (BAA); Samborobon near Gral. Lavalle, *Haumann 31-1630* (POM); Mar Chiquita, *Lanfranchi 1822* (SI).

Specimens from outside of South America (naturalized):

United States. New Jersey, Camden, with ballast, *Martindale in 1866* (GH).

India. Himalaya, cultivated at Almorah, *Duthie in 1900* (K), *Strachey & Winterbottom* (K).

Nepal. Cultivated (K).

Australia. QUEENSLAND: Noosa Heads, *Johnson in 1951* (NSW 135152). NEW SOUTH WALES: N of Raymond Terrace, *Coans in 1961* (NSW 65373); Nelson Bay, *Lithgow in 1965* (NSW 135153); Princess Highway at crossing of Minimurra River, 1 mi S of Albion Park, 1970, *Raven et al. 25887, 25896* (MO, NSW); Centennial Park, Sydney, *Johnson in 1971* (NSW 135154).

Old specimens from plants cultivated in gardens:

Erlangen, Germany, Herb. *Schreber in 1779* (M). Paris, Herb. *Cambessèdes in 1781* (MPU). Vienna, Austria, *in 1806* (W-14035). Schönbrunn at Vienna, *in 1814* (W). Karlsruhe, Germany, *in 1817* (W). Dresden, Germany, *in 1822* (W; as *O. villosa* Thbg.). Munich, Germany, Herb. *Zuccarini in 1832* (M). Munich, *in 1842* (M).

Oenothera mollissima reported in literature from outside its natural area:

Venezuela. Pittier et al. (1947: 258; no material seen!); Vareschi (1970: 247–249, fig. 77; the illustration which is said to be *O. mollissima*, represents *O. tetraptera*, Cav., *Oenothera* sect. *Hartmannia*.)

Oenothera mollissima has two chromosomal complexes derived from *O. affinis* but is so different from that species in its small flowers and distinctive habit that it is best regarded as a distinct entity (Tandon & Hecht, 1955, 1956). Hybrids between *O. mollissima* and *O. affinis* or other chromosomally homozygous species yield progenies in which the two classes of plants differ from one another only trivially, as shown by Haustein (1952). In some strains of *O. mollissima*, both complexes give rise to small-flowered progenies in various combinations; in others, one has genes for a flower size approximating that of *O. affinis*. The small-flowered trait is dominant over the large-flowered one.

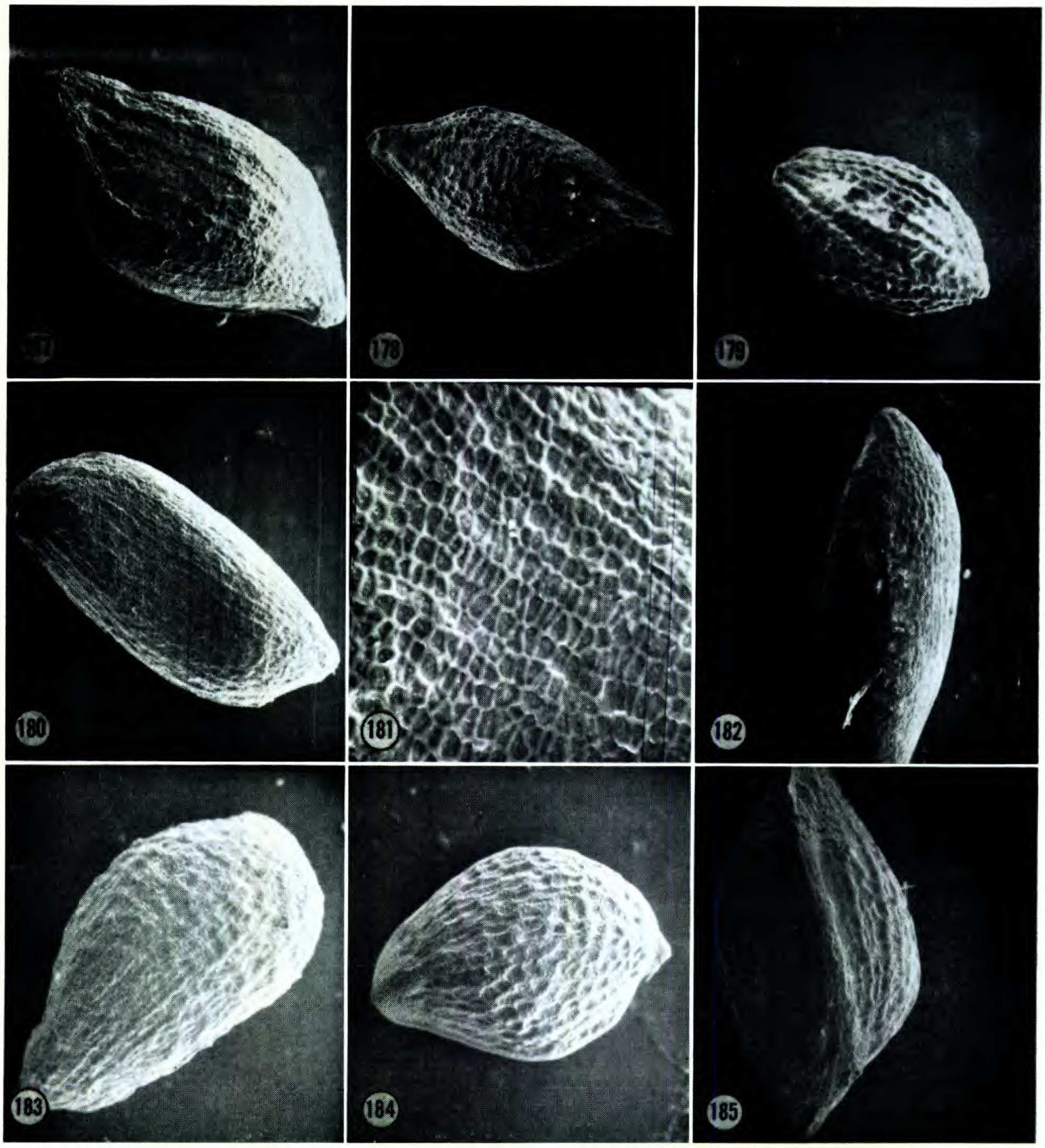
With *O. mollissima* I have included complex heterozygotes (for example, *Santarius 214, 221*) which are, on the basis of their broader leaves and longer floral tube, intermediate to *O. affinis*. Whether such populations have originated by hybridization between the two species and then become stabilized, or actually represent an intermediate stage in the evolution of complex heterozygosity, is not known.

Growing in the same populations as typical *O. mollissima* are often found forms which have apparently originated by introgression with the densely pubescent form of *O. odorata* which occurs in the Province of Buenos Aires. The introgression manifests itself in the lower stature, denser pubescence, undulate leaf margins, and shorter floral tube of these plants. It is not desirable to segregate them taxonomically, however, since they always occur mixed with other plants typical of *O. mollissima* and are best regarded as constituting a part of that species. The very high degree of self-pollination in this species leads to the stabilization of numerous distinctive lines both in the field and in the experimental garden, a veritable feast for the geneticist. Despite this, occasional outcrossing does occur and leads to recombination within the populations, as well as rare interspecific hybridization, which seems to have been of importance in enriching the variability of the species.

22. **Oenothera rivadaviae** Dietrich, sp. nov.—FIGS. 10, 63–64, 135.

Herba ut videtur annua, erecta vel prostrata, rosulata, simplex vel ramis prostratis vel ascendentibus e rosula, caulis principalis 3–7 dm longus. Plantae sparse strigulosae, dense vel sparse villosae, denseque vel sparse glanduloso-pubescentae. Folia rosulae linearia vel angustissime elliptica, acuta, lamina in petiolum gradatim decrescens, 10–15 cm longa, 0.4–0.7 cm lata; folia caulina linearia vel anguste oblanceolata, acuta, basi anguste cuneata vel acuta, sessilia, 4–10 cm long, 0.5–0.8 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi truncata vel subcordata, quam capsulam subtentam longioria vel brevioria, 2–5 cm longa, 0.5–1 cm lata; folia ad margines exigue ad valde undulata, plerumque irregulariter obtuseque serrata. Inflorescentia ramosa. Tubus floralis 1–1.5 cm longus. Gemmae ambito oblongae vel lanceolatae, virides, saepe rubellae, 0.5–1 cm longae, 2.5–4 mm crassae; apices sepalorum divergentes vel erecti, 2–3 mm longi. Petala latissime obovata, 0.6–1.5 cm longa, canarina vel citrina. Stylus brevis, stigmate sub anthesi antheris circumdatus. Ovarium 1.5–2 cm longum. Capsula 3.5–6 cm longa, 2–3 mm lata. Semina ambito anguste elliptica vel elliptica, 1.4–1.8 mm longa, 0.5–0.8 mm crassa. Numerus gameticus chromosomicus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants probably annual, erect or prostrate, forming a rosette, unbranched or with prostrate or ascending side branches from the rosette, the main stem 3–7 dm long. Plants sparsely strigillose, densely or sparsely villous, and densely or sparsely glandular-pubescent. Rosette leaves linear to very narrowly elliptic, acute, gradually narrowed to the petiole, 10–15 cm long, 0.4–0.7 cm wide; cauline leaves linear to narrowly oblanceolate, acute, narrowly cuneate to acute at the base, sessile, 4–10 cm long, 0.5–0.8 cm wide; bracts narrowly lanceolate to



FIGURES 177–185. Scanning electron micrographs of seeds of taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia* (continued).—177. *O. longiflora* subsp. *grandiflora* (Argentina, Corrientes, *Krapovickas & Cristóbal 11293*).—178. *O. indecora* subsp. *indecora* (Uruguay, Maldonado, *Santarius 150*).—179. *O. indecora* subsp. *bonariensis* (Argentina, Buenos Aires, *Santarius 275*).—180. *O. affinis* (Uruguay, Montevideo, *Santarius 193*).—181. *O. affinis* (*Santarius 193*).—182. *O. mollissima* (Uruguay, Montevideo, *Santarius 2*).—183. *O. elongata* (Bolivia, La Paz, *Santarius 2026*).—184. *O. punae* (Argentina, Tucumán, *Santarius 1742*).—185. *O. verrucosa* (Peru, Arequipa, *Santarius 2068*).

lanceolate, acute, truncate to subcordate at the base, longer or shorter than the capsule they subtend, 2–5 cm long, 0.5–1 cm wide; leaves slightly to markedly undulate at the margins, mostly irregularly serrate with blunt teeth. Inflorescence branched. Floral tube 1–1.5 cm long. Buds oblong to lanceolate in outline, green, often flushed with red, 0.5–1 cm long, 2.5–4 mm thick; apices of the sepals divergent or erect, 2–3 mm long. Petals very broadly obovate, 0.6–1.5 cm long, rich yellow to pale yellow. Anthers 4–6 mm long. Filaments 6–8 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.8–3 cm long. Stigma lobes 4–5 mm long. Ovary 1.5–2 cm long. Capsule 3.5–6 cm long, 2–3 mm thick. Seeds narrowly elliptic to elliptic in outline, 1.4–1.8 mm long, 0.5–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–February.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 18 July 1969. Source: Argentina, Prov. Chubut, gravelly and sandy places in Villa Balneario Rada Tilly, ca. 14 km S of Comodoro Rivadavia, 24 Jan. 1968, *K. A. Santarius 913* (MO-2155717, holotype; DUSS, M, isotypes).

Distribution (Fig. 230): So far known only from a few stations in the provinces of Buenos Aires, Chubut, and Santa Cruz, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Dunes about 2 km SE of Argerich in the research terrain of the Universidad del Sur, 37 km W of Bahía Blanca, *Santarius 401** (CTES, DUSS, M, MO). CHUBUT: Gravelly and sandy places in Villa Balneario Rada Tilly, ca. 14 km S of Comodoro Rivadavia, *Santarius 913*, 918, 923*, 924*, 925*, 930, 935, 936* (DUSS; 923 also CTES; 925 also M; *913, 923, 925* also MO).

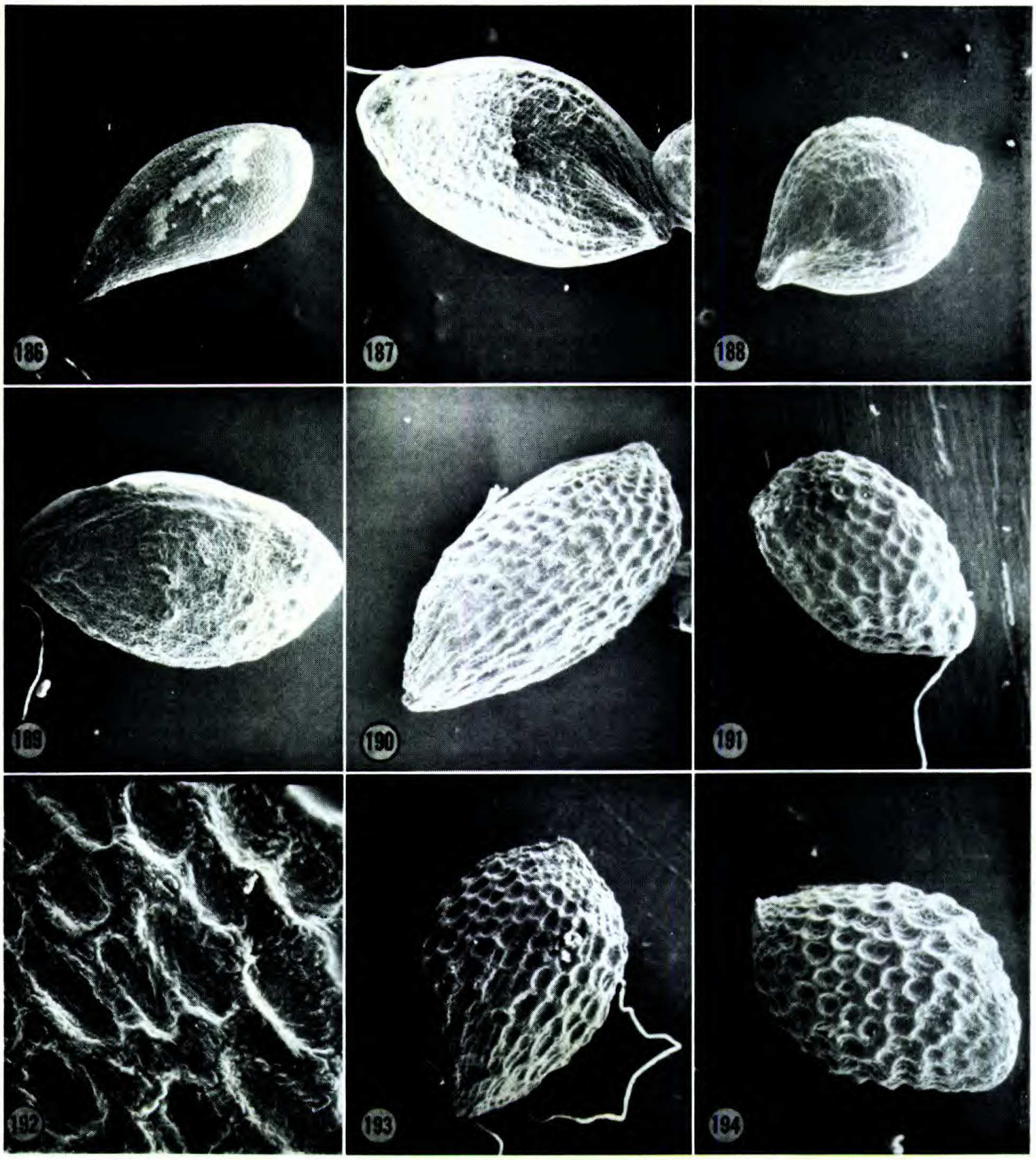
Additional specimen examined:

ARGENTINA. SANTA CRUZ: Comandante Piedrabuena, *O'Donell 3921* (LIL).

Oenothera rivadaviae seems clearly to be a complex heterozygote, the parents of which were *O. mendocinensis* and *O. odorata*. Hybridization with these two homozygous parental species yields plants indistinguishable from them and others indistinguishable from *O. rivadaviae*. The sporadic distribution of this species seems to result from its independent origin following hybridization between its parents at widely separated localities. It may be separated from *O. mendocinensis* by its sparser strigillose pubescence and wider bracts, and from *O. odorata* by its much smaller flowers and narrower capsules.

23. **Oenothera stricta** Ledeb. ex Link ("*striata*"), Enum Pl. Hort. Berol. 1: 377. 1821. H. F. Link misspelled Ledebour's epithet as "*striata*" in publishing the species.—FIGS. 4, 67–72, 136–138, 220–221.

Erect annual or perhaps sometimes biennial herb, rarely decumbent or nearly prostrate, forming a rosette, unbranched or with a branched main stem and side branches arising obliquely or arching upward from the rosette, 3.5–15 dm tall. Plant ± strigillose, especially below, and densely to sparsely long- and short-villous as well as glandular-pubescent. Rosette leaves narrowly elliptic to oblanceolate, acute, gradually narrowed to the petiole or sessile and narrowly cuneate to acute at the base, 10–25 cm long, 0.8–2.5 cm wide; cauline leaves very narrowly elliptic to lanceolate, acute, acute to rounded at the base, sessile, 6–18 cm long, 0.6–2.5 cm wide; bracts narrowly lanceolate to ovate, acute, sessile, truncate to subcordate at the base, 2–3.5 cm long, 0.7–1.5 cm wide, mostly shorter than the capsules they subtend, rarely subequal to them; leaves plane or slightly undulate at the margins, remotely or densely serrate, the teeth blunt or sharp; margins of the bracts usually reddish. Inflorescence simple or branched.



FIGURES 186–194. Scanning electron micrographs of seeds of taxa of *Oenothera* sect. *Oenothera* (continued).—186. *Oenothera coquimbensis* (Chile, Atacama, *Jiles 2160*).—187. *O. arequipensis* (Peru, Arequipa, *Scolnik 1019*).—188. *O. arequipensis* (Peru, Arequipa, *Johnston 3556*).—189. *O. featherstonei* (Peru, Lima, *Macbride & Featherstone 270*). —190. *O. nocturna* (Peru, Lima, *MacHanrish 13*).—191. *O. laciniata* subsp. *pubescens* (Peru, Ayacucho, *Santarius 2235*).—192. *O. laciniata* subsp. *pubescens* (Peru, Junín, *Santarius 2189*). —193. *O. laciniata* subsp. *laciniata* (United States, Missouri, *Russel in 1898*, MO).—194. *O. grandis* (United States, Texas, *Lindheimer 406*, MO).

Floral tube 2–4.5 cm long. Buds narrowly oblong to oblong or lanceolate in outline, green or yellowish green, often flushed with red, 1.2–3 cm long, 0.3–1 cm wide; apices of the sepals erect or divergent, 1–3 mm long. Petals broadly obovate to very broadly obovate, often with a red spot at the base of each one, 1.5–3.5 cm long. Anthers 5–11 mm long. Filaments 10–20 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.8–6 cm long.

Stigma lobes 3–6 mm long. Ovary 1.3–2 cm long. Capsule 3–5 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.3–1.8 mm long, 0.5–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I).

Neotype: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Chile, Prov. Concepción, airport of Concepción, end of 1959, *H. Nodt* (MO-2155718, holotype; CTES, DUSS, M, isotypes).

Distribution (Figs. 230, 231, 235): In Chile from the province of Coquimbo to Isla Chiloe. On the east side of the Andes in the following provinces of Argentina: Neuquén, Río Negro and Chubut, and in the provinces of Chaco, Córdoba, San Luis, and Buenos Aires. The localities for subsp. *stricta* in Ecuador (Quito) and Peru (Lima) must represent stations where the plant is adventive, as is often the case on other continents.

Oenothera stricta has originated as a complex heterozygote between *O. odorata* and *O. ravenii*.

KEY TO THE SUBSPECIES

1. Petals 2.5–3.5 cm long; buds 2–3 cm long, 7–10 mm thick .... 23b. subsp. *altissima*
1'. Petals 1.5–2.5(–3.5) cm long; buds 1.2–1.7 cm long, 3–7 mm thick.
  2. Pubescence shaggy; bracts towards the apex of the stem erect; leaves remotely and bluntly serrate .... 23c. subsp. *argentinae*
  2'. Pubescence not shaggy; bracts towards the apex of the stem spreading; leaves mostly sharply serrate .... 23a. subsp. *stricta*

23a. **Oenothera stricta** subsp. **stricta**.—FIGS. 4, 136, 220.

O. propinqua Spach, Nouv. Ann. Mus. Hist. Nat. 3: 343. 1835. LECTOTYPE: Chile, Prov. Valparaíso, rocky and sandy places along Río Quillota, 1829, *Bertero 1186* (P; LE, NY, P, W, isolectotypes). In his protologue, Spach states that he grew plants from Bertero's seeds, but no corresponding cultivated material has been seen.

O. brachysepala Spach, Nouv. Ann. Mus. Hist. Nat. 3: 345. 1835. TYPE: Chile, Prov. Valparaíso, Quillota, *Bertero 1186* (P, holotype, F and GH, photographs).

O. bracteata Philippi, Anales Univ. Chile 2: 394. 1862. TYPE: Chile, Prov. Curico, Vichuquén near Llico, Dec. 1861, *Landbeck* (SGO, holotype, GH, NY and POM photographs); Linnaea 33: 69. 1864.

O. arguta Greene, Fl. Francisc.: 212. 1891. TYPE: United States, California, Monterey Co., Monterey, July 1891, *Michener* (NDG).

O. propinqua var. *sparsiflora* Philippi, Anales Univ. Chile 84: 631. 1893. TYPE: not located.

O. valdiviana Philippi, Anales Univ. Chile 84: 634. 1893. LECTOTYPE: Chile, Prov. Valdivia, Huchuim, 27 Jan. 1887, *R. A. Philippi* (SGO, holotype, GH, NY and POM photographs).

O. glabrescens Philippi, Anales Univ. Chile 84: 631. 1893. LECTOTYPE: Chile, Prov. Arauco, Lebu, Mar. 1883, *R. A. Philippi* (SGO, holotype, F, GH, NY and POM photographs); Munz, Amer. J. Bot. 22: 661. 1935.

Onagra arguta (Greene) Small, Bull. Torrey Bot. Club 23: 172. 1896.

Oenothera bracteata var. *glabrescens* (Philippi) Reiche, Anales Univ. Chile 98: 476. 1897.

O. mollissima L. var. *valdiviana* (Philippi) Reiche, Anales Univ. Chile 98: 477. 1897; Reiche & Philippi, Fl. Chile 259. 1898.

O. stricta Ledeb. ex Link var. *propinqua* (Spach) Reiche, Anales Univ. Chile 98: 478. 1897; Reiche & Philippi, Fl. Chile 260. 1898.

Onothera polymorpha H. Lév. race *stricta* (Ledeb. ex Link) H. Lév., Monogr. Onoth. 363. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.

O. polymorpha race *propinqua* (Spach) H. Lév., Monogr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.

O. polymorpha race *mollissima* (L.) H. Lév. var. *brachysepala* (Spach) H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909.

Oenothera mollissima subsp. *propinqua* (Spach) Thell., Mitt. Bot. Mus. Univ. Zürich 58: 390. 1912.

O. odorata "Pearce" Cleland, Jap. J. Genet. 43: 332. 1968.

Plants 2.5–10 dm tall, the pubescence not shaggy. Rosette leaves 10–15 cm long, 0.8–1.3 cm wide; cauline leaves 6–10 cm long, 0.6–1 cm wide; bracts 2–3 cm long, 0.7–1.2 cm wide; leaves usually thicker and more sharply serrate than in the other subspecies. Internodes between the capsules 2–4 cm long. Floral tube 2–4.5 cm long. Buds 1.4–1.7 cm long, 3–5 mm thick; apices of the sepal 1–3 mm long. Petals 1.5–2.5(–3.5) cm long. Anthers 7–11 mm long. Filaments 10–20 mm long. Styles 3–6 cm long. Stigma lobes 3–5 mm long. Capsule 3–4 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.4–1.8 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: Northern area, October–May; southern area, October–March.

Distribution (Fig. 230): In Chile from the province of Coquimbo to Isla Chiloé, and on the east side of the Andes only at Lago Nahuel Huapí in the province of Río Negro, Argentina. The localities in Ecuador (Quito) and Peru (Lima) represent escapes from cultivation, as do those on other continents.

Specimens examined from cultivated plants:

CHILE. COQUIMBO: Pisco del Elqui, *Stubbe in 1961** (CTES, DUSS, M, MO). Rivadavia, *Solbrig 3385** (CTES, DUSS, M, MO). VALPARAÍSO: "El Granizo" near Limache, *Göpel in 1961** (CTES, DUSS, M, MO). At the old church in eastern part of Valparaíso, *Göpel in 1961* (CTES, DUSS, M, MO). CONCEPCIÓN: At Río Bío-Bío between Chiguayante and Gualquí, *Mancia in 1965** (CTES, DUSS, M, MO). At Río Bío-Bío near Concepción, *Stubbe in 1960** (CTES, DUSS, M, MO). Airport of Concepción, *Nodt in 1959** (DUSS, M, MO). BÍO-BÍO: Fundo "El Paraíso" near the Monte Aguila, *Göpel in 1962** (CTES, DUSS, M, MO). Los Angeles-Quillaico, *Göpel in 1962** (CTES, DUSS, M, MO). CAUTÍN: Quepe near Temuco, at the railroad near the Río Quepe, *Stubbe in 1960** (CTES, DUSS, M, MO). At the upper current of Río Allipén, on volcanic ashes near Volcán Llaima, *Göpel in 1961** (CTES, DUSS, M, MO). Fundo Walker at Río Trancura N of Volcán Villarica, *Stubbe in 1960** (CTES, DUSS, M, MO). Fundo Saelzer at the S shore of Lago Villarica, *Stubbe in 1960** (CTES, DUSS, M, MO). At Río Allipén SE of Volcán Llaima, *Mittak & Rühm in 1961** (CTES, DUSS, M, MO). VALDIVIA: On dunes near Mehuín, *Nodt in 1959** (CTES, DUSS, M, MO); *Nodt in 1959** (DUSS).

PERU. LIMA: Surco near Lima, *Diers 1091** (CTES, DUSS, M, MO).

*Hecht 1964-8**, source unknown (CTES, DUSS, M, MO). *O. stricta* "Santa Barbara," source unknown, *Cleland 1967-403** (CTES, DUSS, M).

Representative specimens examined:

CHILE. COQUIMBO: Talahueri near Ovalle, *Geisse in 1889* (SGO). ACONCAGUA: Zapallar, *Behn 22800* (CONC). VALPARAÍSO: Quillota, *Philippi in 1856* (W). Between Horcones and Ventana, *Simon 290* (RSA). Limache, *Looser 2008* (GH). Las Zorras, *Harshberger 3391* (NY). Between Curacavi and Casablanca, 600 m, *Killip & Pisano* (RSA, US). Mirasol near Algarrobo, *Kausel 3414* (LIL). Valparaíso, *Sandeman 251* (BM); *Valentin 120* (S); *Maximowitsch 28* (LE); *Mertens* (LD, LE). Río Aconcagua near Caleta de Concón, *Moore in 1884* (SGO). Concón, *Philippi in 1866* (SGO-052879). Viña del Mar, *Philippi in 1882* (BM); *Hicken 263* (SI). Quintero, *Pählmann in 1912* (LD). SANTIAGO: Colina, *Gay 1232* (SGO). San Antonio, *Gay 289* (P); *Valentin in 1921* (S). COLCHAGUA: *Landbeck in 1860* (SGO). CURICO: Cordillera, El Plandion, pass to Argentina, *Bürger in 1903* (GOET). Llico near Vichuquén, *Philippi 613a* (SGO). MAULE: *Kuntze in 1892* (NY). Cauquenes, 1,000–1,650 m, *Ball in 1905* (K). Constitución, *Reiche* (SGO). LINARES: Panimávida, *Philippi in 1885*

(BM); *Holway 224* (US). Longavi, *Schönemann in 1888* (SGO). ÑUBLE: St. Facelco, 520 m, *Pfister 8692* (CONC). Between Curanipe and Buchupureo, *Cox in 1962–1963* (SGO). Hacienda Los Mercedes near Chillán, *Ruiz in 1925* (POM). Puente El Roble near Bulnes, *Parra & Rodriguez 107* (CONC). CONCEPCIÓN: Fundo Trinitaria near Concepción, *Pfister 2166* (CONC). Concepción, *Dombey in 1782* (P); *Neger in 1893–1896* (M); *Jaffuel 3995* (GH); *Mertens* (LE). Hualpén near Concepción, *Barros 6474* (US); *Ricardi 658* (LIL). Río Bío-Bío, *Scott Elliott 86* (BM, NY). Isla Sta. María, *Eights* (US). San Pedro, *Villarod 32162* (CONC). Isla Quiriquina, *Ricardi 10938* (CONC). Coronel, *Ochsenius in 1866* (BR, GOET). Talcahuano, *Hill 162* (K). Lota, *Philippi 610* (SGO). BÍO-BÍO: Fundo Tambillo near Nacimiento, *Pfister 719* (CONC), *186* (LIL). Antuco, *Poeppig in 1829* (M). ARAUCO: Arauco, *Pennell 12920* (F, GH, NY, S, SGO, US). Isla Mocha, *Behn 25366* (CONC). MALLECO: "San Lorenzo" near Angol, *N.N. in 1933* (UC). Mininco, *Schwabe 13338* (CONC). Collipulli, *Ricardi 7455* (CONC). Curacautín, *Burkart 9454* (LIL, SI). Renaico, *Philippi in 1887* (SGO-052830). CAUTÍN: Río Pedregoso near Toltén, *Friedrich 3797* (CONC). Río Zuapa, *Middleton in 1905* (BM). Bajo Imperial, *Middleton in 1906* (BM, G). Gral. Lopez near Temuco, *Sandeman 346* (BM). Temuco, *Claude-Joseph 1843* (US). VALDIVIA: *Philippi in 1888* (K); *Calvert in 1914* (BM); *Buchtien in 1900* (US). San Juan, *Philippi in 1865* (SGO-052881). Niebla near Valdivia, *Buchtien in 1899* (US) (as *O. mollissima* var. *sabulosa* Buchtien). Ranco, *Philippi in 1887* (SGO-052860). Futronhue, *Philippi 613d* (SGO). Cerro Llifén, *Marticorena 63* (CONC); *Boelcke 254* (SI). Bellaviste in the valley of Río Trumas, *Lechler 416* (GOET, K, P). CHILOÉ: Chacao, *Bartulin 12462* (CONC). Isla Chiloé, *Ruiz* (POM); *Nr. 126* (SGO-052883). Castro, *Philippi in 1880* (SGO-052862). Río Palena, *Delfin in 1887* (SGO).

ARGENTINA. RÍO NEGRO: Lago Martín Steffen, *Boelcke 6236* (BAA). Nahuel Huapí, Arroyo Los Cornelios in the valley of Río Limay, *Boelcke & Hunziker 3628* (BAA, MO). BUENOS AIRES: Bahia Blanca, near the port, *Reineck in 1899* (L) (adventive).

ECUADOR. Parque de Ibarra, 2,225 m, 1949, *Solis 13390* (F).

PERU. Rimac valley near Lima, 700 m, 1954, *Rauh-Hirsch 115* (RSA).

Specimens from outside of South America:

UNITED STATES. CALIFORNIA: Monterey Co., *Heller in 1903* (MO).

MEXICO. College garden at Morelia near Michoacán, *Arsène in 1908* (Z).

HAWAII. Maui, Olinda, *Degener in 1927* (MO). Hawaii, Haleakala crater near Holua caves, 1927, *Degener 2254* (K). Haleakala, ca. 2,450 m, 1930, *John 10341* (K); 1940, *Mebold 26664* (M). Kilauea, 1935, *Mebold 20960* (M).

SCOTLAND. Skin works near Selkirk, 1911, *Hayward 1060*, 1913, *1065* (E); 1966, *Webster 10959* (E).

WALES. Aberdovy, *Melville in 1919* (BM), 1919, *Melville 48* (E); 1928, *Britton 3390* (K); 1948, *Taylor 1342* (K). Glamorgan, *Cumming in 1922* (BM, K). SOMERSET: *Duthie in 1869* (BM). Burnham, *Melville in 1873* (E); *Thompson in 1898* (BM, E, K); *Fogitt in 1932* (BM); *Alston in 1949* (BM). Warwick, *Bromwick in 1870* (BM). Berrow, *Davis in 1879* (K); *Fogitt in 1921* (BM).

ENGLAND. BEDFORD: Patton, 1950, *Dony 1221* (K); 1966, *Webster 10942* (E). CHESHIRE: Bickley, *Beer in 1902* (BM). CORNWALL: Gwennap, *Davey in 1903* (E). Par, *Medlin in 1920* (K); *Mebold in 1924* (M). Coverach, *Druce in 1926* (BAS). DEVON: Laira near Plymouth, *Blitt in 1863* (BM). Dawlish Warren, *Redgrove in 1937* (BM); *Proctor in 1952* (LISE). DORSET: Wareham, *Fawett in 1884* (BM); *Linton in 1893* (BM). HAMPSHIRE: Bournemouth, *Alston in 1944* (BM). Blackmoor, 1966, *Webster 10900* (E); 1968, *Lousley 3207*, *3262* (BM). KENT: Catford, *Lowne in 1910* (K). Sandwich Bay, *Meinertshagen in 1932* (BM); *Townsend in 1948* (K); 1961, *Butler 268* (BM). Castle near Sandwich, *Reid in 1975* (BM). Richborough, *Mill in 1860* (K). MIDDLESEX: Twickenham, Clifton Road, *in 1867* (BM). Wandsworth in London, *Forbes in 1837* (BM). NORFOLK: Jarmouth, *Linton in 1879* (BM, K); *Bichham in 1901* (K). SURREY: Croydon, *Bennett in 1873* (E). Bisley Railway, 1958, *Burkill 1639* (E). ISLE OF WIGHT: *Fawett in 1879* (BM); *Jackson in 1894* (K); 1933, *Koster 775* (K); *Townsend in 1951* (K). CHANNEL ISLANDS: Guernsey, *L'Ancresse in 1884* (BM); *Balfour-Brown in 1950* (BM). Jersey, *Watson in 1864* (BM); *Gray in 1894* (BM); 1920, *MacAlister Hall 772* (E); 1954, *Duncan 775* (E).

IRELAND: WEXFORD: Rosslare, *Druce in 1926* (BM).

FRANCE. VIENNE: Châtellerault, *Chabaipeau in 1860* (K, P). LOIRE-ATLANTIQUE: Bourgneuf, *Gad. in 1896* (BM). VENDÉE: Challans, *Portineaux in 1897* (BM). L'Aiguillon, *Foucaud in 1879* (LY); 1911, *Hibon 1461-3* (P). GIRONDE: Bègles, *Neyraut in 1892* (MPU). Pauillac, 1928, *Jallu 461-4* (MPU). LANDES: Capbreton, *Foucaud in 1880* (LY); 1913, *Hibon*

1461-3 (P). Parentis-en-Bors, 1962, *Retz 49626* (LISE). BASSES PYRÉNÉES: St. Jean de Luz, *Barbey in 1883* (Z). Bayonne, 1883, *Blanchet 546* (LISU, LY, MPU, P). Jetée de Boucaud, *Foucaud in 1883* (LY); *Fourés in 1909* (MPU). AVEYRON: Villefranche, *Bras in 1882* (P). HÉRAULT: Castelneau near Montpellier, *Barrandon in 1858, in 1862* (BAS). Sète, *Neyraut in 1887* (MPU); *Cabans in 1933* (MPU). VAR: La Garde-Freinet, Défends du Refrène, 1900, *Bertrand 4725* (HBG, LY, MPO, P), *in 1901* (FR), *in 1903* (LY). Grinaud, *Hibon in 1920* (P). Île d'Aurigny, *Corbière in 1888* (M). MANCHE: Normandie, St. Sauveur-de-Pierrepont, *Corbière in 1893* (LY). FINISTÈRE: Bretagne, *Roscoff, Miciol in 1890* (LY). CHARENTE MARITIME: Montendre, *Foucaud in 1876, 1897 and 1898* (LY). For hybrids with *Oenothera longiflora* subsp. *longiflora* see p. 514.

Italy. Viareggio, *Ball in 1866* (K); *Caldesi in 1880* (LD); *Lévier in 1882* (P); *Gibelli in 1886* (GOET, LY, MPU); *Mori in 1886* (LD); *Knetsch in 1903* (Z); 1908, *Fiori 1316* (BM, E, K, LY, Z).

Portugal. Figueira, *Mariz in 1882* (COI); 1885, *Goltz de Carvalho 825* (COI, LISE, LISU); *Costa in 1933* (COI); *Silva in 1940* (LISE); *Matos in 1948* (C); 1966, *Reis Moura 706* (COI). Ovar, 1951, *Silva et al. 4563* (LISE); 1966, *Merxmüller & Grau 21497* (M). Caldas da Rainha, *Murray in 1889* (BM). Moita, *da Cunha in 1882* (LISU); *Jorge & Mendez in 1917* (LISU); 1942, *da Silva 140* (LISE); 1954, *Rainha 2762* (LISE); *Fernandes et al. in 1961* (COI, LD). Sintra, 1944, *Rainha 46*, 1950, *1983* (LISE). Martigança, 1956, *da Silva et al. 5727* (LISE). Colares, *da Cunha in 1943* (LISU). Cuitra, *dos Santos in 1909* (LISU). Rocha, *Choffat & Daveaux* (MPU). Mizarella near Guarda, *Ferreira in 1885* (COI). Villar Formoso, *Mariz in 1900* (COI). Marinhais, 1946, *Garcia & Souza 918* (COI).

Madeira. Cerro de S. Roque, *Mandon in 1865–1866* (G, K).

Spain. Gigón, *Bourgeau in 1864* (C). Lá Coruña, *Guardi in 1888* (BM). San Sebastian near Guipuzcoa, 1895, *Gandoger 186* (C, COI, K). Prov. Gaditana, near Linea de Concepción, 1895, *Porto & Riga 639* (B). Gibraltar, Linea sand hills, *Wolley-Dod in 1912* (BM). Almoreima near Algeciras, 1924, *Ellman & Hubbard 631* (K). Puerto de Santa María near Cadíz, 1929, *Ceballos 2184* (BM, Z); 1968, *Merxmüller & Lippert 23327* (M). Banks of Río Pobones in Andalusia, 1955, *Brinton Lee 87* (BM).

Germany. Port of Ludwigshafen, *Zimmermann in 1910* (BAS). Kettwig, *Bonte in 1912* (BAS). Rheinweiler near Basel, Herb. *Fischer* (M).

U.S.S.R. European part of USSR, spontaneous in 1964 in a potato field belonging to the Botanical Garden of the University of Moscow, *Skortsov 10188* (DS, MHA). Not to be regarded as a regular member of the adventive flora of European Russia.

Japan. Cultivated, Yokohama, *in 1862* (BM). Kir, 1875, *Rein 20* (GOET). Kyoto, *Rein* (BM, HBG, M); *Hikko in 1877* (HBG). Tokio, Dokwanyama, *Drake in 1881* (P). Harima near Hondo, *Arimoto in 1903* (MO). Kyoto, 1907, *Dunn 8706* (K). Aboshi, 1912, *Schwarz 110* (Z). Honshu, Ashiya, *Fox in 1912* (BM). Kiushu, Hakozaki near Fukada, 1928, *Ichikawa 62* (BM, P). Honshu, Imazu river, 25.6 mi W of Hiroshima, *Charette in 1953* (MO). Niigata, *Drake 52* (P). Yokoka, *Drake* (P).

Pakistan. North-West Himalaya, Murree, *Saunders in 1915* (K); 1918, *Stewart 4039* (RAW).

India. Nilghiri, 1840, *Perrotet 408* (P); 1850, *Hohenacker 1146* (K); *Gamble in 1886* (K). Ootacamund near Madras, ca. 2,300 m, 1882, *Brandis 551* (HBG). Punjab, near Banasar, 1885, *Drummond 24435* (K). Punjab, 1922, *Drummond 24434* (K). Himalaya, at the railway between Suni hill and Tulogk, *Rich in 1916* (K). Kashmir, vicinity of Dalhourie, ca. 2,350 m, 1917, *Stewart 2140* (K). Almora, 1,560 m, 1928, *Parker 2021, 2128* (K). Between Kodai Channel and Pulneys, *Bourne in 1898, 1899* (K); *Foreau in 1960* (K).

Ceylon. Roadside near Ambawella, 1932, *Simpson 2577* (BM).

Java. 1915, *N.N. 107, 120* (K). Tjibodas, Mt. Pangrango, rare, 3,000 m, 1948, *Djambari 317* (L); 1950, *van Ooststroom 13339* (L).

Australia. WESTERN AUSTRALIA: Lower Swan River near Bayswater, *Morrison in 1907* (BM). Bayswater, *Howard 231* (K). Katanning, *Dowell in 1954* (PERTH). Woodman's point, 1961, *Aplin 1071* (PERTH). Claremont, *Steward in 1961* (NSW-135207). Nicholson Road near Cannington, 1961, *George & Marchant 3155* (PERTH). 19 mi SE of Nyabing, 1962, *Newbey 400* (PERTH). Between Borden and Abbany, 1965, *Anway 573* (PERTH). Jerramungup, *Spercer & Fievez in 1971* (PERTH). SOUTH AUSTRALIA: Murrumbidgee, *Nolan in 1841* (MEL). Port Elliot, *Hussey in 1893* (MEL). Mt. Lofty near Adelaide, *in 1897* (MEL). Murray Bridge, *Maiden in 1907* (NSW-135206). Adelaide, *Kaspiew in 1951* (BREM). Wiltunga on Northern York Peninsula, 1966, *Copley 114* (K). Mt. Lofty Range, Balhannah 25 km SE of Adelaide, 1966, *Eichler 18902* (K). Mt. Gambier, 1966, *Wilson 646* (C, MEL).

W shore of Lake Albert, 14 mi W of Meningie, 1967, *Willis 622* (MEL). VICTORIA: Upper Wimmera River near Stawell, *Matthews in 1893* (MEL). Wangaratta, *Weir in 1905* (MEL). Wimmera, *Walter* (MEL-58120). 4 mi NW of Shepparton, between Angustown and Wahoo, *Ackland in 1963* (UPS). 5 mi W of Ararat, 1964, *Muir 3390* (MEL). Red Cliffs, *Henshall in 1964* (MEL). Patchewolluk 11.7 mi N of Hopetoun, 1968, *Belcher 1624* (MEL). NEW SOUTH WALES: Balnarand, 1878, *Lucas 75* (MEL). Filba, *Reader in 1880* (MEL). Riverside near Coonabarralaan, *L. in 1883* (BM). Hume River, *Scott in 1883* (MEL). Turon River, 1885, *Lauterer 40* (MEL). Wagga, *Fletcher in 1888* (NSW-135215). Kogarah, *Campfield in 1893* (NSW-135238). Springfield, 25 mi SW of Cobar, *Andrae in 1895* (MEL-58123). Barbes Creek near Tallong, *Rumsey in 1898* (NSW-135240). Jenolan Caves, *Blakely in 1900* (NSW-135231). Orange, *Boorman in 1906* (NSW-135236). Bega, *Ziethen in 1906* (NSW-135228). Richmond, *Carne in 1906* (NSW-135242). Blackheath, *Maiden in 1908* (NSW-135233). Emu plains, *Hamilton in 1912* (NSW-135241). Wallendbeen, *Beakwell in 1913* (NSW-135219). Bathurst Farm, *Noble in 1914* (NSW-135235); *Brett in 1914* (NSW-135234). Hill Top, Southern Line, *Cheed in 1915* (NSW-135237). Tinga, *Boorman in 1917* (NSW-135222). Blue Mountain, *N.N. in 1919* (MEL-58109). Rylstone, 1920, *Morton 5865-20* (NSW). Tumut, *Redford in 1921* (NSW-135214. Cocketgedong near Jerilderie, *Sibb in 1921* (NSW-135224). Wondabyne to Woy Woy, *Blakely in 1922* (NSW-135243). Junee Distr., *Nugent in 1923* (NSW-135216). Harden, *Rodway in 1924* (NSW-135218). Wallangra, *Rodway in 1929* (NSW-135223). Cullerin, 25 mi W of Goulburn, *Simpson in 1935* (NSW-135229). Armidale University Grounds, *Davis in 1941* (NSW-15230). Morivale to Wellington, *Shelley in 1946* (NSW-135212). Narrabeen Lake, *Johnson in 1946* (NSW-135239). Carlaminda, *Castin in 1948* (NSW-135227). Near Wellington, *Dunk in 1950* (MEL-58103). Narrhari, *Moore in 1952* (NSW-134226). Albury distr., *Glenfield in 1953* (NSW-135213). Near Kootingal, 8 mi ENE of Tamworth, 1954, *Kelso & Goode 64* (NSW-135220). Menindee, *Constable in 1955* (K, MO, NSW-38446). Near Wyong, 1958, *Salasoo 1633* (NSW). Cowro Research Station, *Hill in 1960* (NSW-135210). Canberra, 1962, *Mukee 9666* (NSW). Cootamundra, *Francis in 1963* (NSW-135217). Narrandera, *Leeton in 1963* (NSW-135225). Gunnedah Distr., *Beeson in 1964* (NSW-135221). Michelago to Williamsdale, *Salasoo in 1969* (NSW). Bylong, 33 mi NE of Mudgee, 800 m, 1970, *Raven et al. 25868* (MO, NSW). Pinch River, 39 mi SSW of Jindabyne, 1970, *Pickard & Coveny 2758* (MEL, NSW). QUEENSLAND: *Caves in 1874* (MEL). Silverwood, 1922, *White 1735* (NSW-135209). Mt. Playfair station near Leichhardt, 1964, *Adams 1352* (K). Maryland, *Hickey in 1884* (MEL). Boxbill, *Reader in 1884* (MEL). Lilliput, *in 1913* (MEL). Near Klunzy, *Mueller* (MEL-58115). TASMANIA: Hobart, *Lucas in 1913* (NSW-135208).

NEW ZEALAND. Roturoa, *Chase et al. in 1909* (BM, LIL, K, MO). Swamp near head of Rangaunu, harbour of Puheke Hill, *Mason & Moar in 1949* (AI). Sulphur Springs Bay near Rotoity, *Hurvey in 1949* (AI). Owairaka Park Domain, *Wood in 1950* (AI). Coal Creek, 90 Mile Beach, *Cooper in 1966* (AI). Murimotu at North Cape, *Adams in 1968* (AI). New Zealand, *Hooker in 1870* (K). Paumure, *TFC* (AI).

LIBYA. Distr. Tripolis, Sidi Mesri, 50 m, 1960, *Keith 827* (K).

EGYPT. Near a small village at the Channel *in 1872* (BM).

RHODESIA. Salisbury, on railway, ca. 1,650 m, 1919, *Eyles 1533* (BM, SRGH). Distr. Mtoko, ca. 1,000 m, 1956, *Davies 1926* (K, SRGH). Melsetter village, 1968, *Goldsmith 126-68* (M, SRGH); 1960, *Phipps 2844* (SRGH).

MOZAMBIQUE. Inhaça Island, 23 mi E of Lourenço Marques, 1959, *Mogg 31640* (K).

SOUTH AFRICA. CAPE: Loerie, 1894, *Penther 2150* (M). Distr. Aliwal North, Kraai River, ca. 1,450 m, 1933, *Gerstner 198* (PRE). Distr. East London, 1960, *Comins 2038* (PRE). Distr. Alexandria, Reed Valley, ca. 320 m, 1953, *Archibald 5886* (PRE). Distr. Humansdorp, 1921, *Fourcade 1762* (K). Somerset, *Bowhen* (K). Stellenbosch, 1948, *Parker 4391* (K). Rondebosch, 1934, *Adanson 2232* (BM). TRANSVAAL: Woodbush, 1909, *Jenkins 7201* (PRE). Bokfontein, 1909, *Jenkins 7542* (PRE). Witzies Hoek, 1917, *Junod 14522* (PRE). Grahamstown, 1918, *van Dam 18837* (PRE). Knysna, 1921, *Breyer 23334* (PRE). Along railway near Benoni, 1934, *Bradfield 189* (PRE). Pretoria, 1936, *Reptar 650* (PRE). Bethlehem, *Potgieter 21840* (PRE). ORANGE FREE STATE: Clarence, 1917, *Van Hoepen 18172* (PRE). Gansfontein near Ficksburg, ca. 1,750 m, 1934, *Galpin 13877* (K, PRE). Doornhoek near Bloemhof, *Botha in 1936* (PRE-29489). Bloemfontein, 1951, *Gemmell 6142* (K, PRE); *Hanekom 811* (K, SRGH); 1951, *Potts 6142* (K). *Natal*: 1902, *N.N. 41* (BM). LESOTO: Distr. Tebetebeng, 1957, *Jacot-Guillarmod 2928* (PRE). Maseru, ca. 1,650 m. 1970, *Williamson 19* (K). Leribe, *Dieterlen 169* (P). Province unknown: Wit pootje Kloof, 1948, *Moss 4648* (BM).

Hybrids between *O. stricta* subsp. *stricta* and *O. indecora* subsp. *bonariensis* occur in Australia and Portugal, and are cited under *O. indecora* (p. 522).

Early specimens from plants cultivated in gardens:

Botanical Garden of Dresden, Germany, *Bauer in 1819* (CORD). Copenhagen, Herb. 1820, *Schum. 18* (C). Copenhagen, Herb. 1822, *Schum. 26* (C; as *O. fraseri*). Copenhagen, Herb. 1822, *Schum. 25* (C; as *O. salicifolia*). Botanical Garden of Frankfurt, Germany, seeds from Berlin, *Becker in 1825* (FR; as *O. striata*). Paris, *in 1842* (BR). Leningrad, *in 1848* (LE). Vienna, Austria, *in 1849* (W; as *O. chilensis*).

Oenothera stricta subsp. *stricta* reported in literature from outside of South America:

ENGLAND. Trimen & Dyer (1869: 111, as *O. odorata*); Babbington (1881: 136, as *O. odorata*); Murray (1896: 154, as *O. odorata*); Hanbury & Marshall (1899: 158, as *O. odorata*); Linton (1900: 105, as *O. odorata*); Marquand (1901: 363, as *O. odorata*); Lester-Garland (1903: 113, as *O. odorata*); Davey (1909: 203, as *O. odorata*); Trow (1911: vol. 1: 71, as *O. odorata*); Hooker (1930: 158, as *O. odorata*); Dony (1953); Butcher (1961: vol. 1: 798); Clapham et al. (1962: 480); Perring & Walters (1962).

FRANCE. Gandoger (1886: 49); Corbière (1894: 239); Burnat (1899: vol. 3: 198); Rouy & Camus (1901: 201); Coste (1903: vol. 2: 81); Thellung (1912, as *O. mollissima* subsp. *odorata*); Bonnier (1921: vol. 4: 29); Chassagne (1957: vol. 2: 160); Issler et al. (1965: 357); Raven (1968).

GERMANY. Raven (1968).

BELGIUM. Jean (1975).

SWITZERLAND. Raven (1968).

PORTUGAL. Coutinho (1913: 426; 1939: 508); Sampaio (1946: 408); Raven (1968).

SPAIN. Willkomm & Lange (1880: 181); Willkomm (1893: 219); Colmeiro (1886: vol. 2: 389); Menezes (1914, as *O. odorata*); Wolley-Dod (1914: 42; 1949: 40).

ITALY. Arcangeli (1882: 238); Gandoger (1886); Fiori & Paoletti (1899: vol. 2: 134); Saccardo (1909: 176); Fiori (1925: vol. 2: 14). Zangheri (1976: vol. 1: 421).

U.S.S.R. Shteinberg (1949: 630; 1974, Engl. transl.: 472, as *O. odorata*); Raven (1968)[4].

MOROCCO. Jahandiez & Maire (1931: 516).

ALGERIA. Quézel & Santa (1963: 639).

ETHIOPIA. Bizzari & Raven (1972: 469).

SOUTH AFRICA. Adamson & Salter (1950: 606); Guillarmod (1971: 215, as *O. longiflora*); Ross (1972: 262).

INDIA. Graham (1839: 75, as *O. mollissima*); Hooker (1879: vol. 2: 582, as *O. odorata*); Fyson (1915: vol. 1: 161, vol. 2: 116, as *O. odorata*); Trimen (1931: 131, as *O. odorata*).

CEYLON. Trimen (1894: 235, as *O. odorata*).

JAPAN. Makino (1949: 290, *tab. 868*).

CHINA. Iconographia (1972, as *O. odorata*).

AUSTRALIA. Black (1909: 63; 1926: vol. 3: 427, as *O. odorata*; 1952: vol. 3: 638); Beadle et al. (1962: 173, as *O. odorata*); Eichler (1965: 243).

NEW ZEALAND. Kirk (1899: 180, as *O. odorata*); Cheeseman (1925: 1073).

UNITED STATES. Munz (1965).

The stations for this subspecies at Lago Nahuel Huapí and the Río Limay in Argentina might represent introductions, like those in Ecuador and Peru, especially since there is a constant flow of tourists from Chile to the national parks in Argentina.

This subspecies is morphologically similar to *O. ravenii* subsp. *chilensis*, itself an entity which includes genes from the other parent of *O. stricta*, *O. odorata*. *Oenothera stricta* can be distinguished from *O. ravenii* subsp. *chilensis*, however, by its longer bracts and less erect habit. In fact, considering the range of variation in the species as a whole, the epithet "*stricta*" is a little unfortunate,

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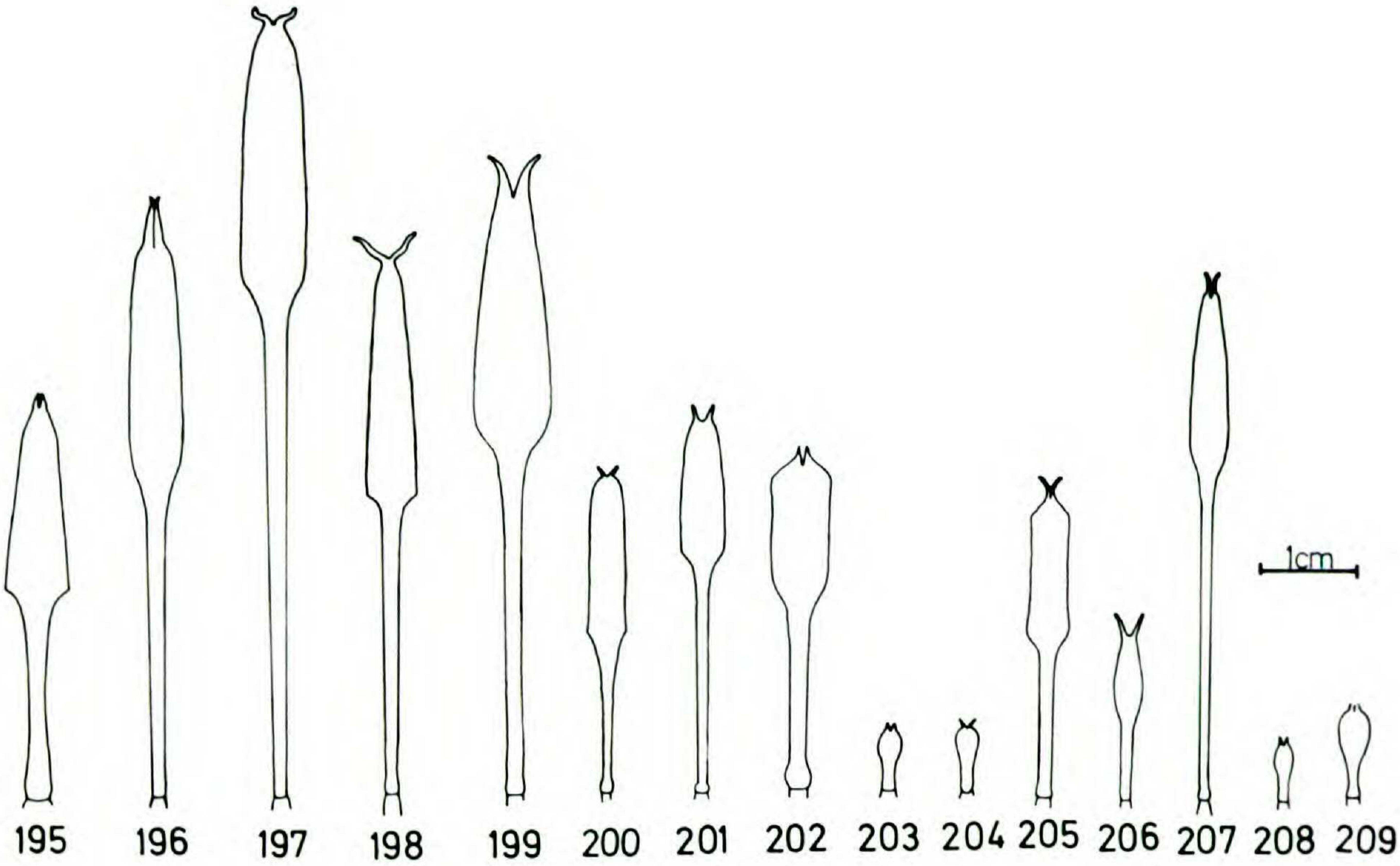
[4] A. K. Skvortsov has kindly informed us that the specimen (*Skvortsov 10188*, DS, MHA) on which Raven (1968) based his record from European Russia was from adventive plants which appeared only in 1964. The species is naturalized in the vicinity of Vladivostok.



FIGURES 195–209. Schematic outlines of buds of taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—195. *O. santarii* (Argentina, Mendoza, *Santarius 1495*).—196. *O. longituba* (Argentina, Tucumán, *Santarius 1736*).—197. *O. longituba* (Argentina, Jujuy, *Fabris 5787*). —198. *O. pedunculifolia* (Argentina, Tucumán, *Santarius 1781*).—199. *O. scabra* (Bolivia, Cochabamba, *Santarius 2003*).—200. *O. scabra* (Peru, Ayacucho, *Santarius 2251*).—201. *O. sandiana* (Peru, Cuzco, *Santarius 2269*).—202. *O. sandiana* (Peru, Junín, *Santarius 2132*).—203. *O. nana* (Peru, Puno, *Santarius 2058*).—204. *O. nana* (Peru, Puno, *Santarius 2055*).—205. *O. villaricae* (Chile, Valdivia, *Göpel in 1961*).—206. *O. cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—207. *O. acuticarpa* (Argentina, Tucumán, *Göpel in 1961*).—208. *O. punae* (Argentina, Tucumán, *Santarius 1742*).—209. *O. verrucosa* (Peru, Arequipa, *Santarius 2073*).

since there are decumbent or nearly prostrate dune and strand forms, such as *Nodt in 1959*.

Especially in the northern part of the range, in the provinces of Coquimbo and Valparaíso, plants with a relatively long floral tube (4–4.5 cm) are frequent (e.g., *Göpel in 1961*, Valparaíso). They correspond more or less to the type of *O. brachysepala* Spach. The most likely explanation for the origin of these plants seems to be introgression from *O. affinis*, either directly or via *O. picensis*, which contains one complex from *O. affinis* and like it grows with *O. stricta* in northern Chile.

23b. **Oenothera stricta** subsp. **altissima** Dietrich, subsp. nov.—FIGS. 67–69, 137, 221.

Plantae 5–15 dm altae; pubes non hirta. Folia rosulae 10–20 cm longa, 1.2–1.7 cm lata; folia caulina 7–15 cm longa, 1–17 cm lata; bractea 2–3.5 cm longa, 0.5–0.7 cm lata; folia remote obtuseque serrulata. Internodia inter capsulas 4–5 cm longa. Tubus floralis 2.5–3.5 cm longus. Gemmae 2–3 cm longae, 7–10 mm crassae; apices sepalorum 1–3 mm longi. Petala 2.5–3.5 cm longa. Capsula 3.5–5 cm longa, 3–4 mm crassa. Semina ambito late elliptica, 1.5–1.8 mm longa, 0.6–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 5–15 dm tall, the pubescence not shaggy. Rosette leaves 10–20 cm long, 1.2–1.7 cm wide; cauline leaves 7–15 cm long, 1–1.7 cm wide; bracts 2–3.5 cm long, 0.5–0.7 cm wide; leaves remotely serrate, with dull teeth. Internodes between the capsules 4–5 cm long. Floral tube 2.5–3.5 cm long. Buds 2–3 cm long, 7–10 mm thick; apices of the sepals 1–3 mm long. Petals 2.5–3.5 cm long. Anthers 6–7 mm long. Filaments 13–18 mm long. Style 3.5–5 cm long. Stigma lobes 3.5–6 mm long. Capsule 3.5–5 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.5–1.8 mm long, 0.6–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–March.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 11 Aug. 1972. Source: Argentina, Prov. Río Negro, NW slopes at Ruta 258 ca. 3 km N of Río Villegas (67 km S of San Carlos de Bariloche), on volcanic ashes and marl, 700 m, 19 Jan. 1968, *K. A. Santarius 798* (MO-2155212, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 231): Along the eastern side of the Andes at low elevations in the provinces of Neuquén, Río Negro, and Chubut, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. PROV. RÍO NEGRO: NW slopes at Ruta 258 ca. 3 km N of Río Villegas, 700 m, *Santarius 798**, *799** (DUSS, MO; *798* also M). N slopes at Ruta 258, 1.5 km S of Río Villegas, on volcanic ashes and marl, 550 m, *Santarius 800** (DUSS, M, MO).

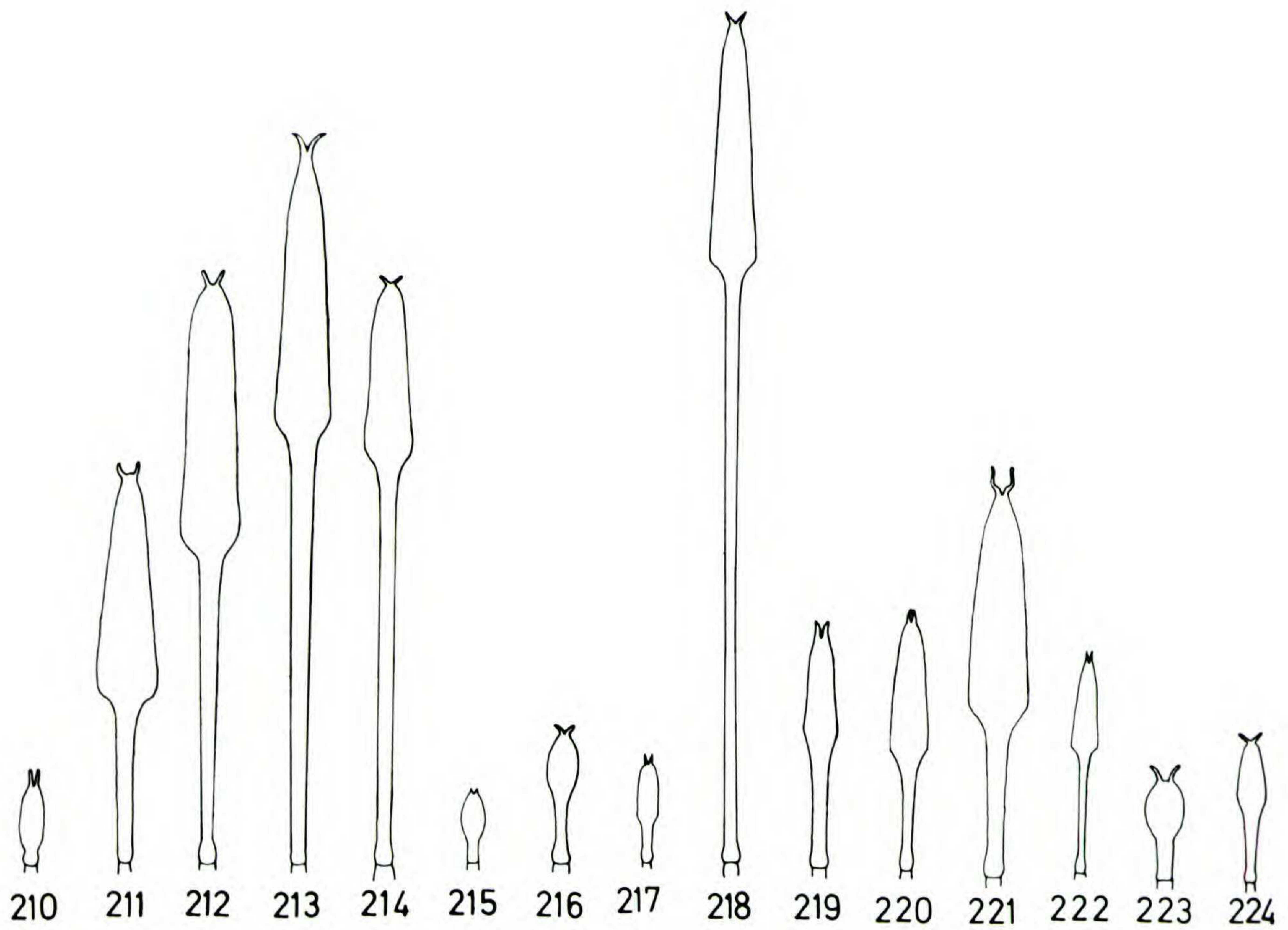
Additional specimens examined:

ARGENTINA. NEUQUÉN: Cascada Maipú, *De Barba 1839* (LIL). Lago Lolog, *De Barba 1794* (LIL). Aluminé, *Soriano 1272* (BAB). Lago Epulafquén, *Dawson & Schwabe 2456* (BAB). San Martín de los Andes, *De Barba 1694* (LIL); *O'Donell 2373* (LIL, NY), *2415* (LIL); *Eskuche 01329* (CTES). Quila Quina, *Cabrera 20521* (LP, P); *Achajonsky 3399* (BAB). Lago Nonthué, Hua Hum, *Valla et al.* (MO). Chos Malal, ca. 650 m, *Comber 169* (K). RÍO NEGRO: S.C. de Bariloche, *De Barba 322* (LIL). Cerro Granito near Bariloche, *Meyer 8244* (LIL). At Ruta 258 near Río Foyel, *Dawson 3290* (BAB, LP). Villegas, *Lourteig & Buchinger 201* (P); *Moreau in 1941* (RSA). El Bolsón, *Meyer 7884* (LIL). CHUBUT: Epuyén near Cushamén, *Muniez 5504* (BAB). Río Corcovado, *Illin 147* (UC).

Considering the relatively large size of its flowers, *O. stricta* subsp. *altissima* may be at an earlier stage in the evolution of complex heterozygosity than is subsp. *stricta*. Since the influence of *O. odorata* is predominant in the phenotype of *O. stricta* subsp. *altissima*, one could assume that this entity arose from the combination of a chromosomally homozygous strain of *O. odorata*, common in the right area, with a genome of *O. ravenii* introgressed with *O. odorata*, the latter probably by way of the Chilean subspecies of *O. stricta*. The direct combination of *O. odorata* with the homozygous, large-flowered *O. ravenii* seems very unlikely, especially since the two are not known to grow together anywhere.

23c. **Oenothera stricta** subsp. **argentinae** Dietrich, subsp. nov.—FIGS. 70–72, 138.

Plantae 5–13 dm altae; pubes hirta. Folia rosulae 10–25 cm longa, 1.5–2.5 cm lata; folia caulina 7–18 cm longa, 0.8–2.5 cm lata; bractea 2.5–3.5 cm longa, 0.7–1.5 cm lata, ad apicem caulis aliquantum imbricata; folia remote obtuseque serrata. Internodia inter capsulae 1.5–3 cm longa. Tubus floralis 2–3.5 cm longus. Gemmae 1.2–1.5 cm longae, 5–7 mm crassae; apices sepalorum 1.5–2 mm longi. Petala 1.5–2 cm longa. Capsula 3–4 cm longa, 3–4 mm lata.



FIGURES 210–224. Schematic outlines of buds of taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—210. *O. mendocinensis* (Argentina, Buenos Aires, *Santarius 411*).—211. *O. odorata* (Argentina, Neuquén, *Santarius 624*).—212. *O. ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul, *Hackbart in 1966*).—213. *O. longiflora* subsp. *grandiflora* (Argentina, Corrientes, *Krapovickas & Cristóbal 11293*).—214. *O. longiflora* subsp. *longiflora* (Uruguay, Colonia, *Santarius 82*).—215. *O. indecora* subsp. *indecora* (Uruguay, Florida, *Santarius 212*).—216. *O. indecora* subsp. *indecora* (Uruguay, Florida, *Santarius 205*).—217. *O. indecora* subsp. *bonariensis* (Botanical Garden Erlangen).—218. *O. affinis* (Argentina, Jujuy, *Santarius 1851*).—219. *O. mollissima* (Uruguay, Montevideo, *Santarius 32*).—220. *O. stricta* subsp. *stricta* (Chile, Concepción, *Stubbe in 1960*).—221. *O. stricta* subsp. *altissima* (Argentina, Río Negro, *Santarius 800*).—222. *O. picensis* subsp. *cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—223. *O. parodiana* subsp. *parodiana* (Uruguay, Florida, *Santarius 207*).—224. *O. nocturna* (Peru, Lima, *Santarius 2333*).

Semina ambito late elliptica, 1.3–1.5 mm longa, 0.6–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 5–13 dm tall, the pubescence shaggy. Rosette leaves 10–25 cm long, 1.5–2.5 cm wide; cauline leaves 7–18 cm long, 0.8–2.5 cm wide; bracts 2.5–3.5 cm long, 0.7–1.5 cm wide, overlapping to a considerable extent towards the apex of the stem; leaves remotely serrate, with blunt teeth. Internodes between the capsules 1.5–3 cm long. Floral tube 2–2.5 cm long. Buds 1.2–1.5 cm long, 5–7 mm thick; apices of the sepals 1.5–2 mm long. Petals 1.5–2 cm long. Anthers 5–7 mm long. Filaments 10–12 mm long. Style 2.8–3.7 cm long. Stigma lobes 3–6 mm long. Capsule 3–4 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.3–1.5 mm long, 0.6–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Buenos Aires, E end of the Sierra del Volcán NW of Puerta El Abra, at km 45 of Ruta 226 between Mar de la Plata and Balcarce, partly grazed terraces between rocks, 150–300 m, 7 Jan. 1968, *K. A. Santarius 346* (MO-2155215, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 235): Known only from a few localities in the provinces of Chaco, Córdoba, San Luis, and Buenos Aires, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: E end of the Sierra del Volcán, at km 45 of Ruta 226 between Mar de la Plata and Balcarce, 150–300 m, *Santarius 346**, *347*, *348*, *350–354*, *355**, *356–367*, *368** (DUSS; *355*, *368* also CTES; *346*, *355* also M; *346*, *352*, *355*, *358*, *368* also MO).

Additional specimens examined:

ARGENTINA. CHACO: Colonia Benítez, *Schulz 792* (POM). Las Palmas, *Jörgensen 2487* (LIL). CÓRDOBA: La Isla near Santa María, *de la Sota 708* (LIL). La Falda near Punilla, *Stuckert 4323* (CORD). Casa Grande near Punilla, *de la Sota 3411* (LIL). Cruz Grande near Punilla, *de la Sota 3634* (LIL). SAN LUIS: Paucanta, *Castellanos 25-864* (POM). BUENOS AIRES: S. Vigilancia near Balcarce, *Jurado 140* (LIL).

This subspecies can be distinguished from the other two by its shaggy pubescence, a characteristic that is often found in *O. ravenii*. The inflorescence of this subspecies is more crowded than in the others, and the internodes between the capsules shorter. It is more heavy-set than in the other subspecies, with the thicker stems and broader leaves especially prominent. In all of these respects, *O. stricta* subsp. *argentinae* approaches *O. ravenii*, which predominates in its genetic makeup in the same way that *O. odorata* does in that of *O. stricta* subsp. *altissima*, a relationship that can easily be understood on geographical grounds.

24. **Oenothera bahia-blancae** Dietrich, sp. nov.—FIGS. 73–75, 139.

Herba annua erecta, rosulata, simplex vel caulis principalis ramosus et ramis oblique e rosula ascendentibus, 5–8 dm alta. Plantae dense vel sparse strigulosae, pilis brevibus longibusque sparse praeditae, et sparse glanduloso-pubescentes. Folia rosulae anguste oblanceolata, acuta, lamina in petiolum gradatim decrescens, 10–15 cm longa, 0.5–1.2 cm lata; folia caulina anguste elliptica vel anguste lanceolata, acuta, sessilia, basi anguste cuneata vel acuta, 5–10 cm longa, 0.6–1.5 cm lata; bractea anguste lanceolata vel lanceolata, acuta, sessilia, basi rotundata vel truncata, 2–3 cm longa, 0.7–1 cm lata; folia plana vel ad margines undulata, irregulariter obtuseque serrata. Inflorescentia simplex vel ramosa. Tubus floralis 1.2–2.5 cm longus. Gemmae ambito oblongae vel lanceolatae, virides vel flavovirescentes, saepe junctura sepalorum tubo florali rubrofasciatae, 0.6–1.2 cm longae, 3–4 mm latae. Sepala saepe fuscorubro punctata; apices sepalorum erecti, 1–2 mm longi. Petala obovata vel latissime obovata, 0.7–1.5 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.3–1.5 cm longum. Capsula (2–)3–4.5 cm longa, 3–4 mm crassa. Semina ambito late elliptica, 1.2–1.5 mm longa, 0.6–0.8 mm crassa. Numerus gameticus chromosomicus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, forming a rosette, with a simple or branched main stem and the side branches arising obliquely from the rosette, 5–8 dm tall. Plants densely to sparsely strigillose, sparsely long- and short-villous, and sparsely glandular-pubescent. Rosette leaves narrowly oblanceolate, acute, gradually narrowed to the petiole, 10–15 cm long, 0.5–1.2 cm wide; cauline leaves narrowly elliptic to narrowly lanceolate, acute, sessile, narrowly cuneate to acute at the base, 5–10 cm long, 0.6–1.5 cm wide; bracts narrowly lanceolate to lanceolate, acute, sessile, rounded to truncate at the base, 2–3 cm long, 0.7–1 cm wide;

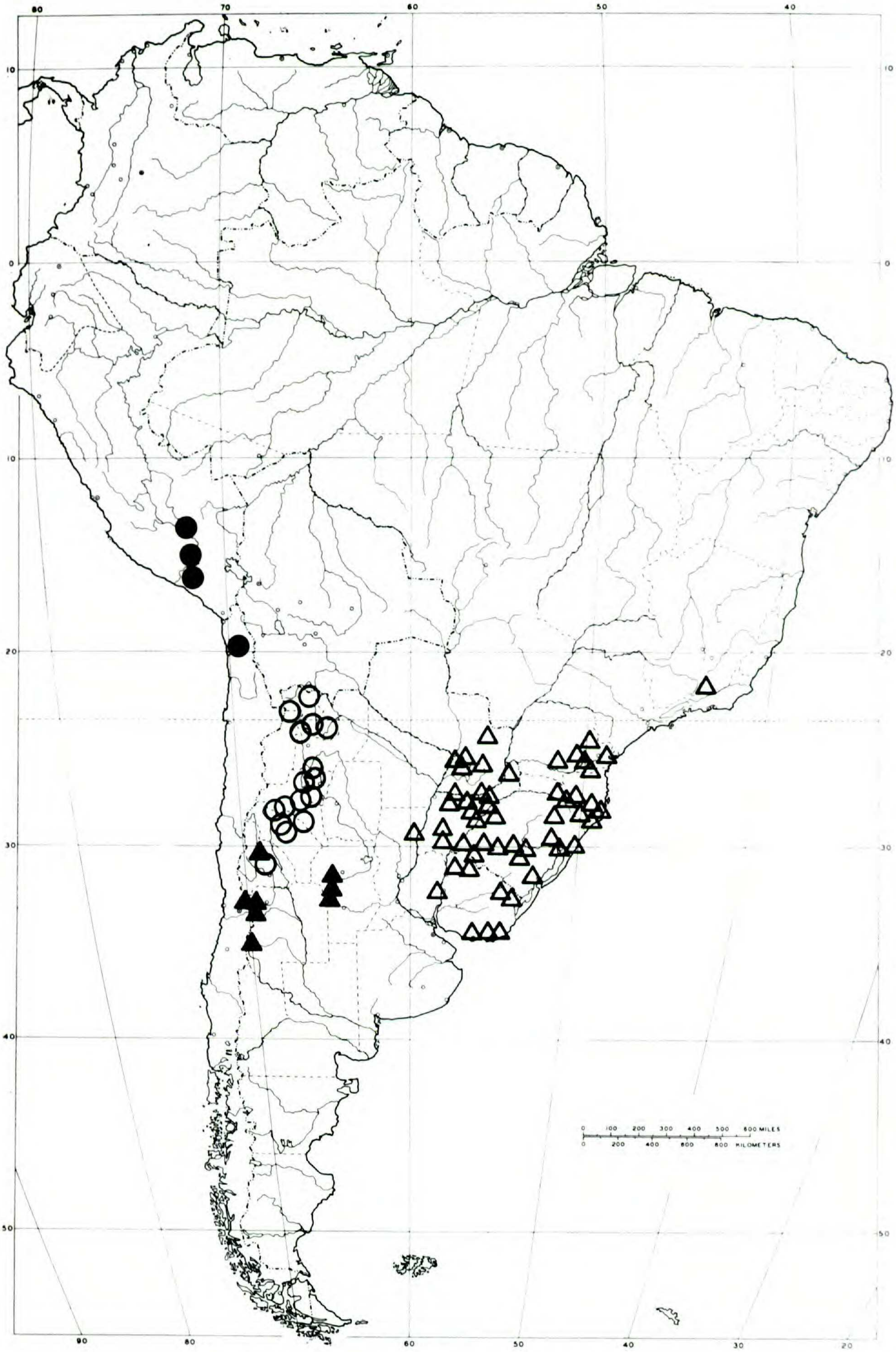


FIGURE 225. Ranges of *Oenothera peruana* (dots), *O. lasiocarpa* (circles), *O. santarii* (filled triangles), and *O. ravenii* subsp. *ravenii* (hollow triangles).

leaves plane or undulate at the margins, irregularly serrate, the teeth blunt. Inflorescence branched or unbranched. Floral tube 1.2–2.5 cm long. Buds oblong to lanceolate in outline, green to yellowish green, often red striped at the junction of the sepals with the floral tube, 0.6–1.2 cm long, 3–4 mm thick. Sepals often flecked with dark red; apices of the sepals erect, 1–2 mm long. Petals obovate to very broadly obovate, 0.7–1.5 cm long. Anthers 4–6 mm long. Filaments 5–10 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.8–3.2 cm long. Stigma lobes 3–4 mm long. Ovary 1.3–1.5 cm long. Capsule (2–)3–4.5 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.2–1.5 mm long, 0.6–0.8 cm wide. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Buenos Aires, dunes ca. 2 km SE of Argerich in the research terrain of the Universidad del Sur, 37 km W of Bahía Blanca, 9 Jan. 1968, *K. A. Santarius 455* (MO-2155721, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 236): Known only from the provinces of Buenos Aires, La Pampa, Neuquén, and Chubut, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Dunes ca. 2 km SE of Argerich in the research terrain of the Universidad del Sur, 37 km W of Bahía Blanca, *Santarius 455**, *457**, *460**, *465* (DUSS; 457 also CTES; *455*, *457* also M, MO). NEUQUÉN: Sandy places in the SE part of the city of Neuquén, *Santarius 542**, *558*, *560*, *569**, *575** (DUSS; *542*, *569* also CTES, M; *542*, *569*, *575* also MO). Sandy and waste places in the irrigation ditches of the farm "Granja LU" in the SE part of the city of Neuquén, *Santarius 567**, *590**, *594*, *595* (DUSS; *590* also CTES, M; *567*, *590* also MO). Stony places at Río Limay, 6 km E of Piedra del Águila, *Santarius 597**, *598**, *604** (DUSS; *598* also CTES, M; *598*, *604* also MO).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: Necochea, *Hicken 4662* (LIL). Laguna Brava near Gral. Pueyrredón, 100 m, *Descole in 1938* (LIL). San Clemente near Gral. Lavalle, *Cabrera 4262* (GH). Bahía Blanca, *Claraz in 1884* (G). Dunes near Bahía San Blas, *Fabris & Schwabe 5012* (LP). Pigué near Saavedra, *Burkart 4713* (MO). Sierra de Curamalal, *Cabrera 5433* (LP). Sierra La Tinta, El Sombrerito, 400 m, *Spegazzini 41* (BAB). Est. Sta. María at Río Colorado near Villarino, *Hunziker 4452* (POM, SI). Campo "La Susana" near Est. Peralta, 320 m, *Huidobro 1177* (LIL, NY, S, SI). Sierra de la Ventana, *Molfino 46137* (BAB); *Gomez 11785* (BAA, MO). LA PAMPA: Guatrache, *Williamson in 1925* (SI). NEUQUÉN: Bajada del Manzano, 20 km S of Zapala, *Ancibor 90245* (BAA). RÍO NEGRO: Choele Choel near Perellaneda, 152 m, *O'Donell 1795* (NY). Dep. Conesa, China Muerte near Laguna del Mate in the valley of Río Negro, 60 km E of Carmen de Patagones, *Krapovickas 2078* (RSA); *Hunziker 479* (CORD, RSA). CHUBUT: Valle de Las Plumas, *Gerling 137* (POM). Cabo Raso, *Müller 24* (CORD). Between Travesia de Rawson and the Cordilleras, *Illin 16* (SI).

It has not yet been possible to analyze the complexes involved in the origin of *O. bahia-blancae* with any degree of certainty. On the basis of the strigillose pubescence and the relatively small leaves, one might suggest that one of the complexes of *O. mendocinensis* is involved, while the other might be an altered complex derived from *O. longiflora* and with genes for smaller flowers than in that species. Such a complex, ultimately derived from *O. longiflora*, is represented both in *O. parodiana* of series *Allochroa* and in *O. cordobensis* of series *Clelandia*.

25. **Oenothera picensis** Philippi, Anales Mus. Nac. Chile, Bot. 1891: 22. 1891. Figs. 65–66, 140–142, 222.

Annual herb with an erect or somewhat decumbent main stem, not forming a rosette, simple or branched near the base, 2–10 dm tall. Plants very densely to sparsely long-villous, the hairs soft, densely to sparsely short-villous and glandular-pubescent. Cauline leaves narrowly elliptic to lanceolate, acute, acute to truncate at the base, sessile, 3.5–10 cm long, 0.5–2 cm wide; bracts narrowly oblong or narrowly lanceolate to narrowly ovate, acute, truncate to subcordate at the base, sessile, 2.5–6 cm long, 0.5–2 cm wide, longer than the capsule they subtend or subequal to them, occasionally shorter; leaves plane or coarsely undulate at the margins, irregularly serrate, the teeth blunt. Inflorescence mostly branched. Floral tube 1.5–4.5 cm long. Buds oblong to lanceolate in outline, 0.7–1.7 cm long, 3–5 mm thick, often red striped at the junction of the sepals with the floral tube. Sepals often flecked with dark red; apices of the sepals 1–2 mm long, mostly erect. Petals broadly obovate to very broadly obovate, sometimes broadly elliptic, 0.7–2.5 cm long. Anthers 5–12 mm long. Filaments 5–15 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2–6 cm long. Stigma lobes 3–6 mm long. Ovary 1–2 cm long. Capsule (2–)2.5–4(–4.5) cm long, 3–4 mm thick. Seeds elliptic to broadly elliptic in outline, 1.2–2 mm long, 0.5–0.8 mm thick, brown. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14, ring of 10 and ring of 4 or ring of 8 and ring of 6 at meiotic metaphase I).

Lectotype: Chile, Prov. Atacama, oasis of Pica, Mar. 1885, *R. A. Philippi* (SGO-52850, GH photograph).

Distribution (Fig. 237): At the foot of the Andes in Argentina in the provinces of Jujuy, Salta, Tucumán, Catamarca, San Juan and Mendoza, and also in the provinces of Buenos Aires, Córdoba, San Luis, and Río Negro; on the western side of the Andes in Chile from the province of Antofagasta to Colchagua. *Oenothera picensis* subsp. *picensis* is adventive on the Juan Fernández Islands and in the provinces of Bío-Bío and Malleco in southern Chile.

Each of the three subspecies of *O. picensis* is made up of chromosomal complexes originating from *O. odorata* on the one hand and *O. affinis* on the other. They must have originated independently from one another, however, judging from their completely distinct areas of distribution. One of the most important characteristics of *O. picensis* is that it forms no rosette, a characteristic that can be traced back to the influence of *O. affinis*, one of its parents. The soft pubescence is also reminiscent of *O. affinis*, whereas the width of the bracts at their base is a characteristic of *O. odorata*.

Key to the Subspecies

1. Plants densely long-villous.
    2. Floral tube 2–4.5 cm long .... 25a. subsp. *picensis*
    2′. Floral tube 1.5–2 cm long .... 25c. subsp. *bonariensis*
1′. Plants not densely long-villous.
    3. Petals 1.5–2.5 cm long .... 25a. subsp. *picensis*
    3′. Petals 0.7–1.3 cm long .... 25b. subsp. *cordobensis*

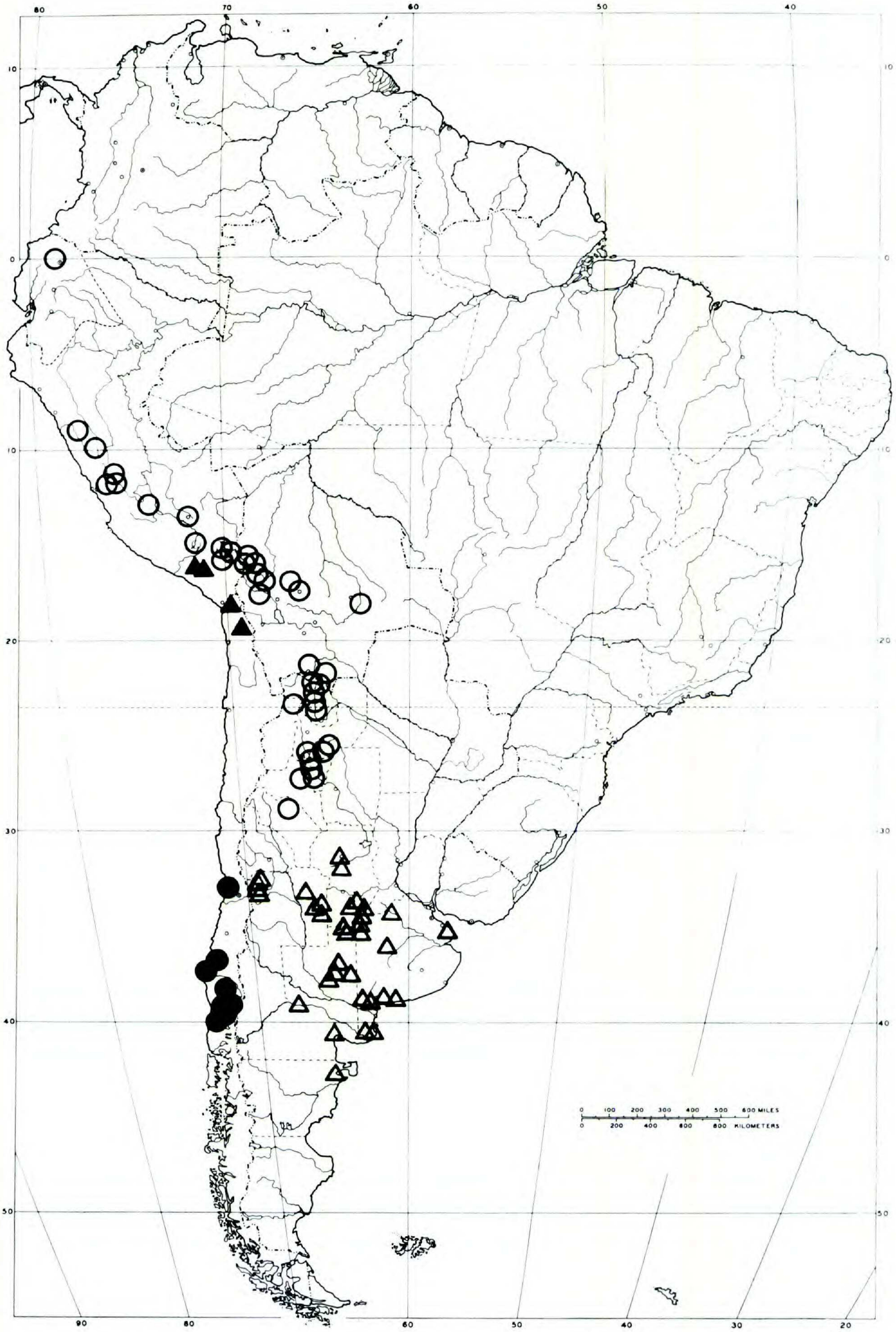


FIGURE 226. Ranges of *Oenothera versicolor* (circles), *O. rubida* (filled triangles), *O. mendocinensis* (hollow triangles), and *O. ravenii* subsp. *chilensis* (dots).

25a. **Oenothera picensis** subsp. **picensis**.—Fig. 140.

O. odorata sensu Gillies ex Hooker, Bot. Misc. 3: 310. 1833, pro parte.
O. mollissima sensu Gillies ex Hooker, Bot. Misc. 3: 310. 1833.
O. mollissima sensu Reiche, Anales Univ. Chile 98: 476. 1897.
O. mollissima sensu Munz, Amer. J. Bot. 22: 659. 1935, pro parte; Revista Univ. (Santiago) 22: 266. 1937, pro parte.
O. affinis sensu Munz, Revista Univ. (Santiago) 22: 267. 1937, pro parte.
O. odorata "Erlangen" Haustein, Z. Indukt. Abstammungs- Vererbungsl. 84: 418. 1952; Cleland, Jap. J. Genet. 43: 332. 1968.
O. mollissima "Uspallata" Tandon & Hecht, Cytologia 21(3): 252. 1956.

Plants 4–10 dm tall. Plants densely to sparsely long- and short-villous, sparsely glandular-pubescent. Cauline leaves narrowly lanceolate to lanceolate, acute, 6–10 cm long, 0.5–1.3 cm wide; bracts lanceolate to narrowly ovate, acute, truncate to subcordate at the base, 3.5–6 cm long, 0.8–1.5 cm wide. Floral tube 2–4.5 cm long. Buds oblong to lanceolate in outline, 1.2–1.7 cm long, 4–5 mm thick. Petals very broadly obovate, 1.5–2.5 cm long. Anthers 7–12 mm long. Filaments 11–15 mm long. Style 3–6 cm long. Stigma lobes 4–6 mm long. Ovary 1.2–2 cm long. Capsule 2.5–3.5 cm long. Seeds elliptic in outline, 1.3–2 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–May.

Distribution (Fig. 237): In Chile from the province of Antofagasta to Colchagua; adventive on the Juan Fernández Islands and in the southern Chilean provinces of Bío-Bío and Malleco; on the east side of the Andes in the provinces of Mendoza and San Juan in Argentina.

Specimens examined from cultivated plants:

CHILE. VALPARAÍSO: Concón to Salinas near the border to Prov. Aconcagua, *Hjertung & Rahn 553** (CTES, DUSS, M, MO). Concón, N of Viña del Mar, *Göpel in 1961* (DUSS, MO).

ARGENTINA. MENDOZA: Uspallata, *Hecht 1964-78** (CTES, DUSS, M, MO). Stony places at Río Mendoza near the bridge of Ruta 7, 10 km S of Uspallata, 1900 m, *Santarius 1549**, *1550** (DUSS; *1549* also CTES, M, MO). On rocks ca. 5 km S of Cacheuta, 23 km N of Luján de Cuyo, 1200 m, *Santarius 1551*, *1553* (DUSS; *1553* also MO). Stony and waste places ca. 2 km N of Tupungato, 1250 m, *Santarius 1554**, *1556*, *1564*, *1565*, *1570*, *1571** (DUSS; *1554*, *1564* also MO). At the road above El Peral, 6 km NW of Tupungato, 1350 m, *Santarius 1576** (DUSS, M, MO).

CULTIVATED: *O.* "*odorata*" from the Botanical Garden in Erlangen, Germany, received 1960* (CTES, DUSS, M, MO).

Additional specimens examined:

CHILE. ANTOFAGASTA: Chuquicamata, *Martin 173* (SI). Toconao, 2,300 m, *Ricardi 2998* (CONC); *Ivanovič 7713* (CONC). ATACAMA: La Pampa, valley of Río del Transito, 1,450 m, *Johnston 5861* (GH, K, POM). Est. Manflas, *Ricardi 3748* (CONC). La Higuerita near San Félix, 1,300 m, *Ricardi 3870* (CONC). Copiapó, *Ricardi 3625* (CONC); *Gigoux in 1885* (GH). Desert of Atacama, *Morong 1105* (F, MO, NY). COQUIMBO: Tulahuén, *Alamo 19175* (CONC). Punitaquí near Ovalle, *Jiles 1936* (CONC). ACONCAGUA: Portillo on road to Mendoza, *Diaz in 1861-62* (SGO). Río Blanco, 1,400 m, *Günther & Buchtien in 1928* (S). VALPARAÍSO: *Bueck in 1843* (HBG); *Wilkes* (NY); *Buchtien in 1895* (US). Olmué near Limache, *N.N. 1901* (HBG). Limache, *Behn 22798* (CONC). Reñaca valley, *Poulsen in 1951* (C). Between Concón and Salinas, *Hjerting & Rahn 553* (C). Viña del Mar to Concón, *Günther & Buchtien in 1928* (HBG). SANTIAGO: *Claude-Joseph 726* (US). Romeral at Río Yezo, *Biese 83* (GH, LIL). Chacayes at Río Yezo, *Biese 139* (LIL). Dunes near El Tabo, *Kohler 229* (CONC). San Antonio, *Looser 924* (SI). Dunes of Llolléo S of San Antonio, *Poulsen in 1952* (C). Valley of Maipo, between Obra and Canelo, *Looser 144-17* (SI). El Manzano near San José de Maipo, 870 m, *Montero in 1927* (GH, K); *Sparre in 1947* (S). Batuco, *Reiche* (SGO-061514); *Looser 2406* (POM), 257 (SI). COLCHAGUA: Talcaregoné, *Gay in 1831* (P). BÍO-BÍO: Trapatrapa (SGO-052829). MALLECO: Sta. Rosa, *Philippi in 1882* (SGO). *Islas Juan Fernández*: *Philippi in 1864* (SGO-052867); *Bertero 1486* (K, P). Masatierra, *Bürger* (GOET); *Skottsberg 141* (S, UPS); *Bock 22801* (CONC). Masafuera, Quebrada Casas, *Meyer 9352* (MO). Province unknown: Aeuleo, *Bertero 446* (W), *464*, *1185* (G, MPU, NY, P). Cerro S. Cristóbal, *N.N. in 1868* (W).

ARGENTINA. MENDOZA: *Jörgensen 131* (C). Mendoza, 800 m, *King 112* (BM); *Sanzin 87* (SI); *Loos 2390* (CORD). San Carlos, *Roig 5178* (CORD); *Covas 3492* (SI). Dep. Tunuyán, Campo de los Andes, 1,800 m, *Paci 713*, *727* (LIL); Barkley *20Mz126* (LIL, NY, P, W). Arroyo La Remonta, 1,500 m, *Melis & Paci 777* (LIL, NY); *Cáceres 76* (LIL, NY). Dep. Las Heras, Quebrada del Toro, 2,000 m, *Calastremé 72032* (BAB). La Gloria, *Ruiz Leal 963* (Leal). Villavicencio, *Burkart et al. in 1942* (SI-14176). Tupungato, *Ruiz Leal 2784b*, *2784* (Leal, POM), *2775* (Leal, LP). Dep. Lújan, Cacheuta, *Ruiz Leal 8734* (Leal, LIL). Potrerillo, 1,500 m, *Semper 401* (LIL); 1,600 m, *Garcia 374* (LIL). Dep. San Rafael, Río Diamante, *Reales 1966* (LIL). Aguo del Sapo, 1,200 m, *Ruiz Leal 7378* (Leal, LIL). Río Atuel, 1,400 m, *Wilczek 410* (G). Between Yagualito and Las Peñas, *Kurtz 5412* (CORD). Cordillera of Mendoza, Cordón de Sta. Elena, *Figueroa 15736* (CORD). Cordilleras, *Jensen-Haarup in 1904* (C, LD, S).

Specimens from plants cultivated in gardens:

Leningrad, seeds from Chile sent by Cuming, *in 1833* (LE). Kew, *in 1880* (K; as *O. holosericea*).

Among the F_1 generation hybrids between *O. affinis* and *O. picensis* subsp. *picensis* there are two classes of plants, one closely similar to each parent. The same occurs in hybrids between *O. odorata* and *O. picensis* subsp. *picensis*. Consequently, the parentage of this particular subspecies seems to be clearly demonstrated.

Since there is no evidence that chromosomally homozygous entities of this series have ever occurred in Chile, it seems most probable that the *O. affinis* complex in *O. picensis* subsp. *picensis* was derived from the complex heterozygous *O. affinis* that does occur in Chile, and that the *O. odorata* complex was derived via *O. stricta*. It is also possible, of course, that *O. stricta* has derived its *odorata*-complex from *O. picensis*. This seems improbable, however, since the *ravenii*-complex of *O. stricta* in Chile is much more widespread than the *affinis*-complex of *O. picensis*, so that one might surmise that the *odorata-ravenii* combination originated earlier than the *odorata-affinis* combination.

From Chile *O. picensis* subsp. *picensis* seems to have migrated over the Uspallata Pass to Argentina, where it seems to form occasional secondary hybrids with the homozygous *O. odorata*, judging by the presence of plants with relatively large flowers in the Argentine portion of the range of *O. picensis* subsp. *picensis*.

25b. **Oenothera picensis** subsp. **cordobensis** Dietrich, subsp. nov.—FIGS. 65–66, 141, 222.

O. mollissima sensu Munz, Physis 11: 282. 1933, pro parte.
Oenothera parodiana sensu Munz, Physis 11: 283. 1933, pro parte; Amer. J. Bot. 22: 662. 1935, pro parte.

Plantae 2.5–9 dm altae, plerumque pilis longis villosis dispersis praeditae, etiam pilis brevibus villosis glandulosibusque praeditae. Folia caulina anguste elliptica vel lanceolata, 3.5–5 cm longa, 0.5–1 cm lata; bractea anguste oblonga ad oblongam vel anguste lanceolata at lanceolatam, 2.5–3.5 cm longa, 0.5–1 cm lata, quam capsulas subtentas breviora vel subaequalia. Tubus floralis 3–4.5 cm longus. Gemmae ambito oblongae vel lanceolatae, 0.7–1.2 cm longae, 3–4 mm crassae. Sepala fusco-rubro saepe punctata; apices sepalorum 1–2 mm longi.

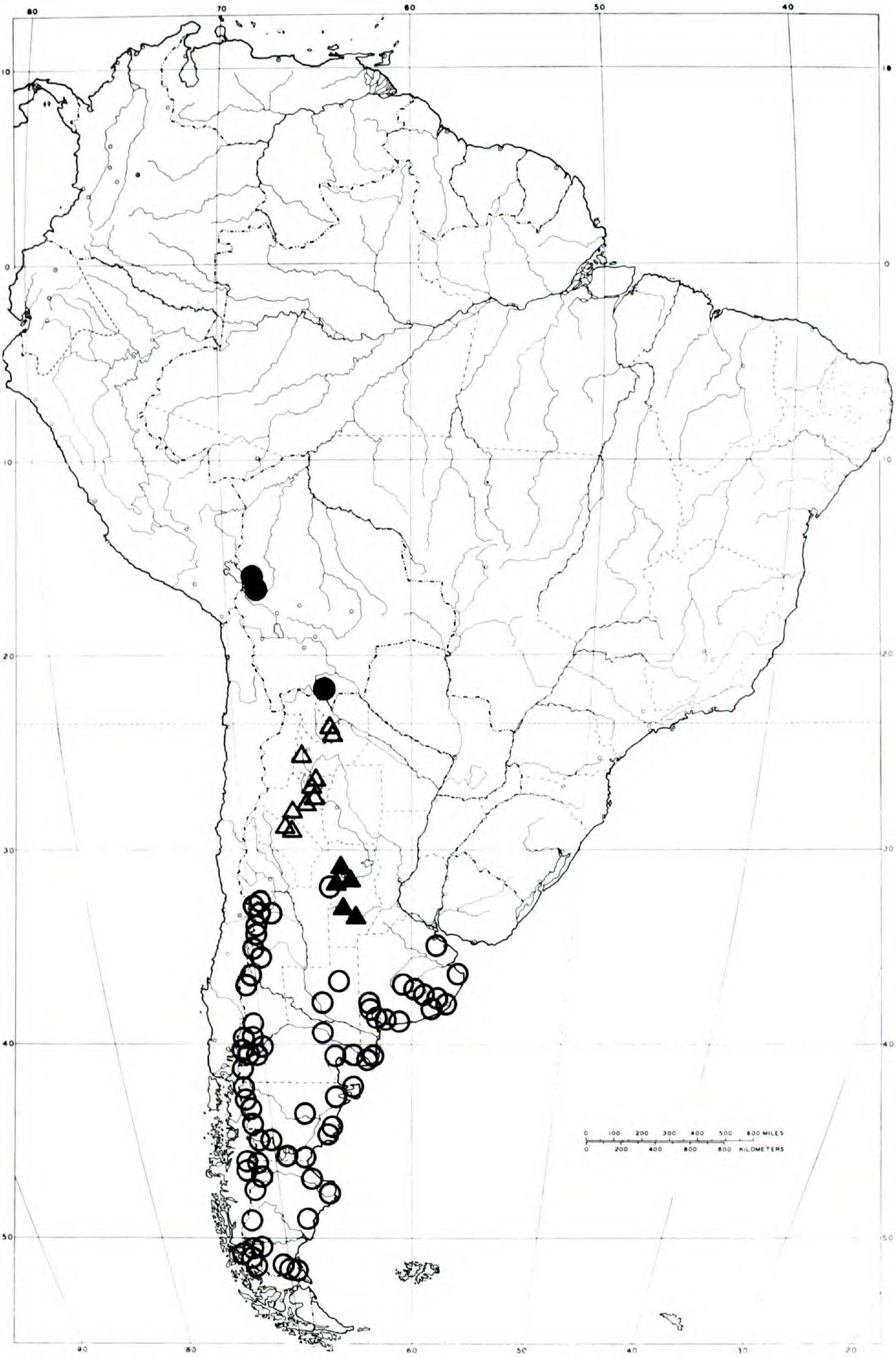


FIGURE 227. Ranges of *Oenothera longituba* (hollow triangles), *O. tarijensis* (dots), *O. odorata* (circles), and *O. cordobensis* (filled triangles).

Petala late elliptica vel late obovata ad latissime obovata, 0.7–1.3 cm longa. Ovarium 1.1–1.4 cm longum. Capsula (2–)3–4(–4.5) cm longa. Semina ambito late elliptica, 1.2–1.7 mm longa, 0.7–0.8 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 2.5–8 dm tall. Usually with scattered long-villous pubescence, but also densely short-villous and glandular-pubescent. Cauline leaves narrowly elliptic to lanceolate, 3.5–5 cm long, 0.5–1 cm wide; bracts narrowly oblong to oblong or narrowly lanceolate to lanceolate, 2.5–3.5 cm long, 0.5–1 cm wide, shorter than the capsules they subtend or subequal to them. Floral tube 3–4.5 cm long. Buds oblong to lanceolate in outline, 0.7–1.2 cm long, 3–4 mm thick. Sepals often flecked with dark red; apices of the sepals 1–2 mm long. Petals broadly elliptic or broadly obovate to very broadly obovate, 0.7–1.3 cm long. Anthers 5–7 mm long, ca. 1 mm wide. Filaments 5–10 mm long. Style 3.5–5 cm long. Stigma lobes 3–4 mm long. Ovary 1.1–1.4 cm long. Capsule (2–)3–4(–4.5) cm long. Seeds broadly elliptic in outline, 1.2–1.7 mm long, 0.6–0.8 mm thick. Self-pollinating and often cleistogamous. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 10 and ring of 4** at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Córdoba, Cuesta de San Roque near Córdoba, ca. 4 km of "Carlos Paz," 19 Dec. 1961, *G. Göpel* (MO-2155410, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 237): At low elevations, up to 1,300 m or rarely ascending to 1,800 m, in the provinces of Jujuy, Salta, Tucumán, Catamarca, Santiago del Estero, Córdoba, and San Luis, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. JUJUY: In the bed of Río Xibi Xibi SE of San Salvador de Jujuy, 1250 m, *Santarius 1805**, *1806**, *1807*, *1809*, *1812*, *1815*, *1816**, *1817*, *1819*, *1822*, *1823*, *1824*, *1828*, *1829*, *1831–1833*, *1835**, *1836*, *1837*, *1840* (DUSS; *1804*, *1806*, *1816*, *1835* also CTES; *1805*, *1806*, *1816*, *1835* also M; *1805*, *1806*, *1809*, *1816*, *1817*, *1824*, *1835* also MO). In the bed of Río Grande N of San Salvador de Jujuy, 1250 m, *Santarius 1845**, *1846***, *1847*, *1848** (DUSS; *1848* also CTES, M; *1845*, *1846*, *1848* also MO). CÓRDOBA: Between Córdoba and Cuesta Blanca, *Göpel in 1961** (DUSS, M, MO). Villa Independencia near Córdoba, *Göpel in 1961** (CTES, DUSS, M, MO). Cuesta de San Roque near Córdoba, *Göpel in 1961** (CTES, DUSS, M, MO). Copina near Córdoba, *Göpel in 1961** (DUSS, M, MO).

Representative specimens examined:

ARGENTINA. JUJUY: *O'Donell 2802* (LIL, NY); *Kuntze in 1892* (NY). León, 1,700 m, *Cabrera et al. 13907* (BAB, LP). Shore of Río Xibi Xibi near San Salvador de Jujuy, 1,260 m, *Arnow 3642* (MO). SALTA: Río Pescado near Orán, *Alberti 71517* (BAB). Campo Quijano near Rosario de Lerma, *Meyer 3586* (F, GH, LIL, NY). Río Vaquero near Caldera, 1,200 m, *Sparre 1231* (S). Lesser near Calitera, 1,950 m, *Filipovicz 440* (LIL). El Ladil near Candelaria, *Montenegro 351* (LIL). Río Concha near Metán, *Herrera 28* (LIL). Quebradas of Río Toro and Río Blanco, *Vattuone 49*, *134* (LIL, SI). TUCUMÁN: Arroyo Itaembé, *Meyer 11484* (LIL). El Timbo near Burroyacu, 600 m, *Venturi 2231* (US). Río Salí near Tucumán, 450 m, *Venturi 898a* (NY). CATAMARCA: *Castillón 1666* (SI). El Chorro near Ancasti, *Rojas Paz 16* (GH, LIL). Sierra de Ancasti, Ruta 66, *Hunziker & Di Fulvio 17097* (CORD). La Banda, *Spegazzini 29285* (BAB). El Portezuelo, *Bartlett 19613* (MICH, US). Dep. Pomán, Sierra de Ambato, between El Rincón and Las Casitas to Cerro Manchado, 2,300–2,500 m, *Hunziker & Arizo 20372* (CORD). Tinogasta, *Ahumada 56* (LIL). Yacutula, *Schickendantz 161* (CORD). El Alto, *Argañaraz 652*, *674* (LIL). SANTIAGO DEL ESTERO: Ojo de Agua, *Balegno 152*, *183*, *1306* (LIL); *Garcia 893* (LIL). CÓRDOBA: Córdoba city, *Stuckert 22108* (CORD, MO). Santa María, 600 m, *Gutierrez 247* (LIL). El Durazno, 1,200 m, *Meyer & Sleumer 15702*

(LIL). Capilla del Monte, *Lanfranchi 633* (SI); *Hossens 210, 400, 427, 694* (CORD). Copina, 1,400 m, *Hieronymus 334* (P), *655* (CORD, GOET). Lago San Roque near Carlos Paz, *Bridarolli 265* (LP). Valle Hermoso, *Huidobro 138* (LIL). Las Rosas near La Falda, *Stuckert 16940, 18925* (G); *Wall in 1946* (S); *Job 506* (NY). Tanti, *Nicora 2923* (SI). Casa Bamba, *Krapovickas 1882* (LIL). Alta Gracia, 1,800 m, *Pierotti in 1944* (LIL, NY, S, US). Las Peñas near Totoral, *Balegno 1169* (LIL). Villa García, *Meyer in 1940* (F). Taninga, *Boelcke 7745* (BAA, MO). Mina Clavero, *Meyer 13386* (LIL). Cruz del Eje, 470 m, *Meyer 13043* (LIL). Unquillo, *Bruch in 1926* (F, NY). Cerro Saúce Punco near Tulumba, 700 m, *Meyer 13100* (LIL). Ascochinga, *Calderon 658* (BAA). Pampa de Achala, 2,200 m, *Hunziker 1402, 1403* (CORD). Cerro de Chaján near Río Cuarto, 500 m, *Hunziker 16504* (CORD). Sierra de Achiras, 800 m, *King 525* (BM). Sierra Chica, La Redución, *Burkart 7327* (SI). Rosario, *Bartlett 20165* (GH, MICH, US). Dean Funes near Ischilin, *Cuezzo 705* (BM, F, LIL, S). Dep. Río Segundo, Manfredi, *Krapovickas 6616* (BAB, CORD, LIL). Cosquín, 730 m, *Rodrigo 275* (NY, US). Villa de María at Río Seco, *Balegno 1458* (LIL). Gral. Paz, *Stuckert 3739* (CORD, G). Salsipuedes near Colón, *Dawson 84* (LP, NY); *Hunziker 1474* (CORD, LIL, RSA). Santa Catalina near Colón, *Dawson 436* (POM). Jesús María near Colón, *Balegno 1487* (LIL). Dep. Calamuchita, Arroyo Calmayo near Soconciro, *Bodenbender in 1925* (CORD). Champaquí, *Reutzell in 1944* (SI). SAN LUIS: Cerro El Morro, Est. La Morena, 1,100–1,400 m, *Hunziker 12589* (CORD, MO). Piedra Blanca near Merlo, 1,000 m, *Grassi 2090* (LIL). Sierra de Comechingones, El Rincón, *Hunziker 11754* (CORD). Encrucijada, *in 1879* (BM). Peñón Colorado, *Castellanos 29-380* (BA, POM). Valley of Río Quines, *Galander in 1882* (CORD). Est. Grande, *Vignati 7* (SI), *587* (LP). Dep. Capital, Portrero de los Funes, banks of Arroyo de los Molles, 980 m, *Lee Anderson 1963* (CORD). Nogoli, *Gez 76* (SI).

Oenothera picensis subsp. *cordobensis* can be distinguished from subsp. *picensis* especially through its smaller flowers, less dense long villous pubescence, and mostly oblong leaves. Evolution in the *affinis*-complex in this entity seems to have proceeded farther in the direction of small flowers than in subsp. *picensis*, judged from the fact that F_1 hybrids between subsp. *cordobensis* and homozygous *O. affinis* consist of two classes of plants, one resembling *O. picensis* with medium-sized flowers, and one a very small-flowered type of plant resembling *O. affinis*.

Introgression of genes from *O. ravenii* or *O. longiflora* is seen in the plants of *O. picensis* subsp. *cordobensis* which have red-flecked sepals or short bracts. This has probably come about by means of occasional hybridization between *O. picensis* and *O. parodiana* which grow with *O. picensis* subsp. *cordobensis* in the province of Córdoba. Evidently, the genes associated with the red flecking of the sepals are in the portion of the chromosomes in which crossing over occurs, for they seem to be transferred readily from one complex to another. *Oenothera ravenii* is the only chromosomally homozygous species in South America which displays this characteristic.

In *O. picensis* subsp. *cordobensis*, the flowers often fail to open at all and are therefore completely cleistogamous. Even though the sepals split apart, they remain attached by their apices, and the petals cannot unfold. In a sense, one could regard this as the ultimate reduction associated with complex heterozygosity, since self-pollination renders the opening of the flowers superfluous.

25c. **Oenothera picensis** subsp. **bonariensis** Dietrich, subsp. nov.—Fig. 142.

O. mollissima sensu Munz, Amer. J. Bot. 22: 659. 1935, pro parte.

Plantae 4–10 dm altae, densissime pilis longis, dense pilis brevibus, denseque pilis glandulosis praeditae. Folia caulina anguste lanceolata vel lanceolata, basi truncata vel subcordata,

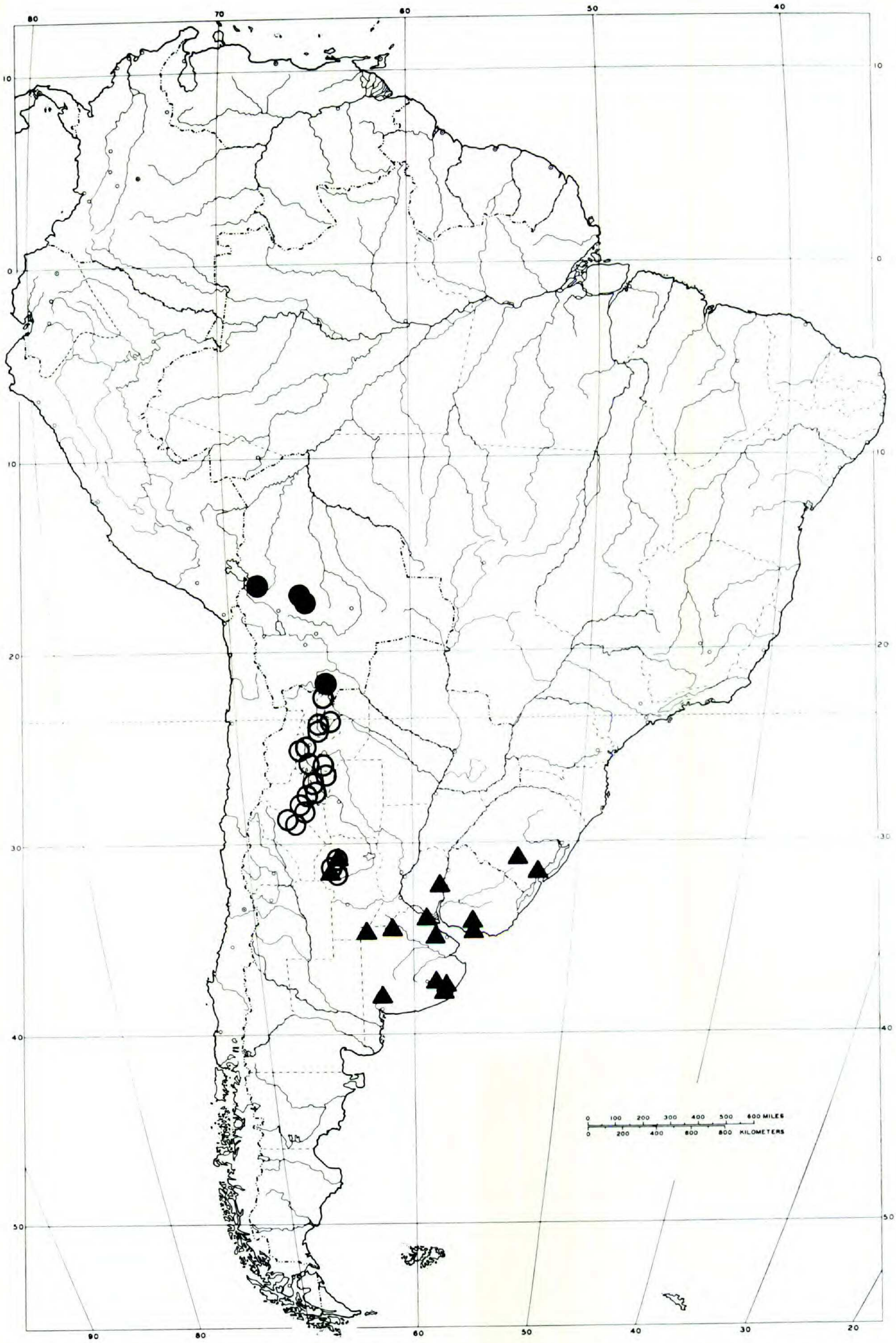


FIGURE 228. Ranges of *Oenothera tafiensis* subsp. *tafiensis* (circles), *O. recurva* (dots), and *O. ravenii* subsp. *argentinae* (filled triangles).

4–10 cm longa, 1.3–2 cm lata; bractea lanceolata vel anguste ovata, 3.5–6 cm longa, 1.3–2.5 cm lata, basi truncata vel subcordata. Tubus floralis 1.5–2 cm longus. Gemmae ambito oblonga vel late oblonga, 0.7–1.2 cm longa, 4–5 mm crassa. Sepala non rubro-punctata; apices sepalorum 1.5–2 mm longi. Petala late obovata vel latissime obovata, interdum late elliptica, 1–1.7 cm longa. Ovarium 1.2–1.5 cm longum. Capsula 2.5–3.5 cm longa, 3–4 mm crassa. Semina ambito elliptica, 1.2–1.8 mm longa, 0.6–0.8 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 4–10 dm tall. Plants very densely long-villous, densely short-villous and glandular-pubescent. Cauline leaves narrowly lanceolate to lanceolate, truncate to subcordate at the base, 4–10 cm long, 1.3–2 cm wide; bracts lanceolate to narrowly ovate, 3.5–6 cm long, 1.3–2.5 cm wide, truncate to subcordate at the base. Floral tube 1.5–2 cm long. Buds oblong to broadly oblong in outline, 0.7–1.2 cm long, 4–5 mm wide. Sepals not red flecked; apices of the sepals 1.5–2 mm long. Petals broadly obovate to very broadly obovate, sometimes broadly elliptic, 1–1.7 cm long. Anthers 5–8 mm long. Filaments 6–10 mm long. Style 2.0–2.7 cm long. Stigma lobes 3–4 mm long. Ovary 1.2–1.5 cm long. Capsule 2.5–3.5 cm long, 3–4 mm thick. Seeds elliptic in outline, 1.2–1.8 mm long, 0.6–0.8 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 8 and ring of 6** at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 11 Aug. 1972. Source: Argentina, Prov. Buenos Aires, N end of the Sierra La Peregrina, S of km 25.5 of Ruta 226 between Mar del Plata and Balcarce, 7 Jan. 1968, *K. A. Santarius 370* (MO-2155204, holotype; CTES, DUSS, isotypes).

Distribution (Fig. 237): Provinces of Buenos Aires and Río Negro, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: N end of the Sierra La Peregrina, S of km 25.5 of Ruta 226 between Mar del Plata and Balcarce, *Santarius 370**, *374*, *389**, *393*, *395*, *397** (DUSS; 383, 397 also CTES; *370*, *389*, *397* also M, MO). Sierra de la Ventana, rocks and stony hills at both sides of the railroad, 1 km NE of La Pileta, 350 m, *Santarius 490**, *500*, *503*, *506*, *508*, *515** (DUSS; *490* also CTES, M; *490*, *500*, *515* also MO). RÍO NEGRO: Stony place at the ferry across the Río Limay at Ruta 237, 75 km SSW of Piedra del Águila, *Santarius 640*** (CTES, DUSS, M, MO).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: Sierra de la Ventana, 300 m, *Huidobro 1320* (BM, LIL, S). Valle de las Vertientes, *Huidobro 1442* (LIL, NY, S, SI). Tornquist, *Visetti 54318* (BAB). Sierra Ventana, *Molfino 31-1632* (POM). Arroyo Sauce Grande, *Bartlett 20032* (GH, MICH, SI, UC). Tornquist, 400 m, *Hunziker 584*, *515* (CORD); *Meyer 14264* (LIL); *Krapovickas 2112* (LIL, RSA); *Rossi & Bachmann 459* (LIL). Cerrito La Ruina NE of Tornquist, *Rossi 466* (LIL). Port of Bahía Blanca, *Hicken in 1899* (POM). Canteras near Tandil, *Huidobro 1721* (LIL, S). Tandil, *Parodi 1682*, *1799* (BAA). Sierras del Tandil, Parque Independencia, *Abbiatti 4207* (LP). Sierra Buenavista near Balcarce, *Hunziker 2309* (POM, SI). Sierra La Vigilancia near Balcarce, *Cabrera 17155* (LP). Cerro "La Peregrina" near Balcarce, *Grondona & Dawson 6339* (BAA); *Eyerdam et al. 23644* pro parte (GH). Mar del Plata, *Valentini 446* (SI). Coastal dunes of Pinamar near Gral. Madariaga, *Boelcke 9040* (BAA, MO). Dunes near Bahía San Blas, *Fabris 5012* (M). Mar Chiquita, *Pelosi 120* (LIL, SI).

Oenothera picensis subsp. *bonariensis* differs strikingly from the other two subspecies in its dense long villous pubescence. The *odorata*-complex of this subspecies is derived from the densely pubescent form of the species that occurs in the province of Buenos Aires. The *affinis*-complex very probably has come by way of *O. mollissima*, but the relatively small buds that are more or less oblong

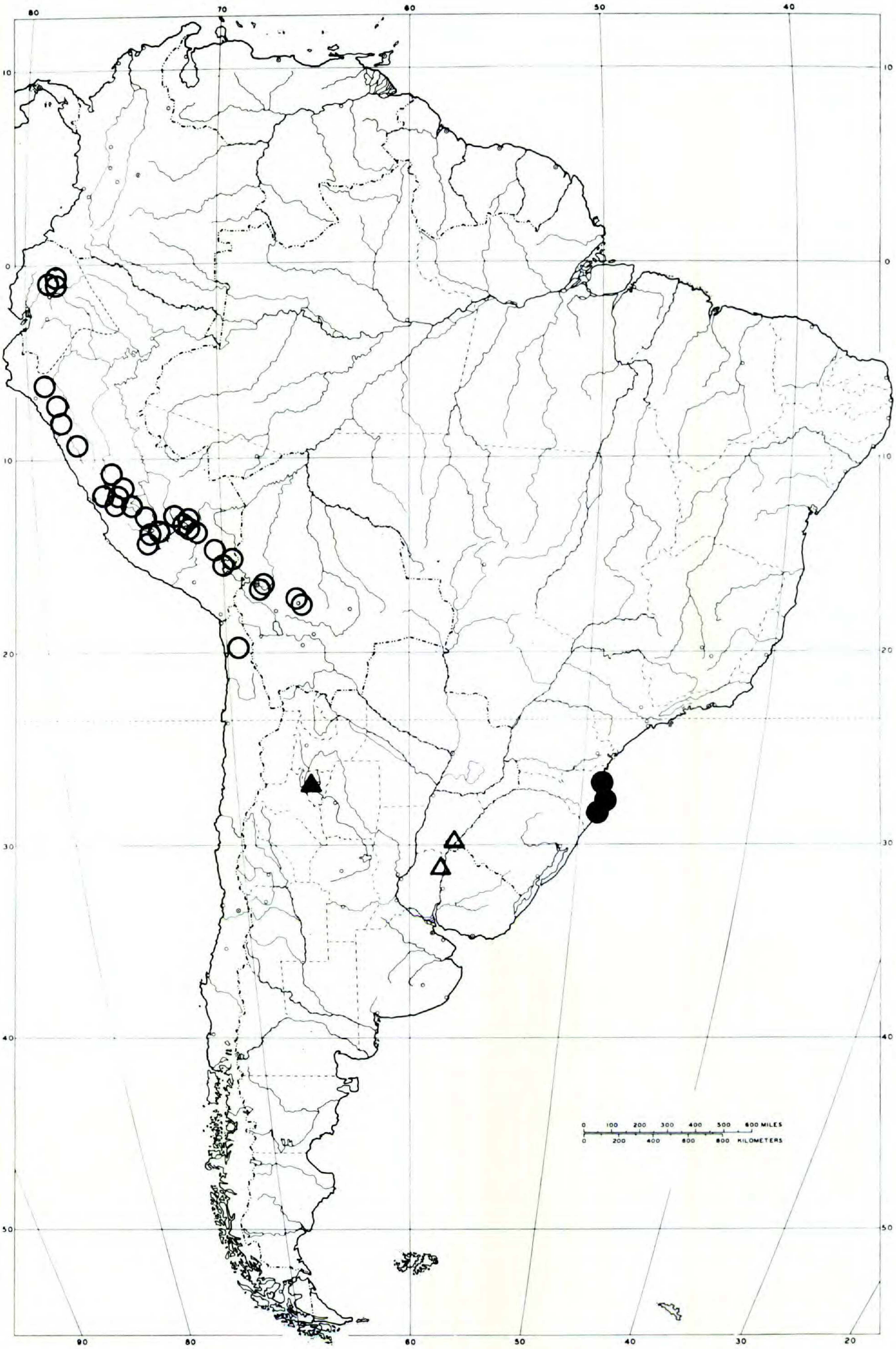


FIGURE 229. Ranges of *Oenothera tafiensis* subsp. *parviflora* (filled triangle), *O. sandiana* (circles), *O. longiflora* subsp. *grandiflora* (hollow triangles), and *O. catharinensis* (dots).

in outline and the short floral tube suggests introgression from *O. indecora* subsp. *bonariensis*.

26. **Oenothera montevidensis** Dietrich, sp. nov.—FIG. 143.

Herba annua, non rosulata, plerumque caule principale oblique vel subdecumbente simplice vel circum basin ramoso 3–5 dm longo. Plantae dense vel sparse pilis longis villosis, densissime pilis brevibus villosus et glandulosis praeditae. Folia caulina cultrata vel lanceolata, acuta, basi acuta vel rotundata, sessilia, 2–4 cm longa, 0.5–1 cm lata; bractea lanceolata vel anguste ovata, acuta, basi truncata, sessilia, quam capsula subtenta breviora vel ad eas subaequalia, 2–2.5 cm longa, 0.5–1 cm lata; folia plana vel ad margines exigue undulata, irregulariter obtuseque serrata. Inflorescentia ramosa. Tubus floralis 1–1.5 cm longus. Gemmae ambito oblongae, 0.5–0.7 cm longae, 3–3.5 mm crassae, flavo-virentes; apices sepalorum 0.5–1 mm longi. Petala latissime obovata, 0.5–0.8 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 0.6–1.6 cm longum. Capsula 2–2.5 cm longa, 2–2.5 mm crassa. Semina ambito elliptica, 1.5–1.6 cm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Annual herb, not forming a rosette, mostly with an obliquely ascending or somewhat decumbent main stem, which is unbranched or branched near the base and 3–5 dm long. Plants densely to sparsely long-villous, also very densely short-villous and glandular-pubescent. Cauline leaves cultrate to lanceolate, acute, acute to rounded at the base, sessile, 2–4 cm long, 0.5–1 cm wide; bracts lanceolate to narrowly ovate, acute, truncate at the base, sessile, shorter than the capsules they subtend or subequal to them, 2–2.5 cm long, 0.5–1 cm wide; leaves plane or weakly undulate, irregularly serrate, the teeth blunt. Inflorescence branched. Floral tube 1–1.5 cm long. Buds oblong in outline, 0.5–0.7 cm long, 3–3.5 mm thick, yellowish green; apices of the sepals 0.5–1 mm long. Petals very broadly obovate, 0.5–0.8 cm long. Anthers 3–5 mm long. Filaments 5–7 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.5–2.2 cm long. Stigma lobes ca. 3 mm long. Ovary 0.6–1.6 cm long. Capsule 2–2.5 cm long, 2–2.5 mm thick. Seeds elliptic in outline, 1.5–1.6 mm long, 0.5–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 8 Aug. 1972. Source: Uruguay, Dep. Montevideo, dunes near Carrasco and Miramar, 26 Dec. 1967, *K. A. Santarius 1* (MO-2155207, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 235): Found only in the departments of Canelones and Montevideo in Uruguay.

Specimens examined from cultivated plants:

URUGUAY. MONTEVIDEO: Dunes near Carrasco and Miramar, *Santarius 1**, *9*, *11*, *12*, *15**, *17*, *18*, *27*, *28* (DUSS; *1* also M; *1*, *9* also MO).

Additional specimens examined:

URUGUAY: MONTEVIDEO: Carrasco, *Rosengurtt 850* (POM); *Courbon in 1856* (P); *Olazarri 205* (LIL). CANELONES: Bank of Arroyo Carrasco, *Rosengurtt B430* (LP, POM).

Superficially, *O. montevidensis* would seem to be a derivative of *O. mollissima*, but it is also very similar to *O. indecora* subsp. *indecora*. It can be distinguished from the latter by its thicker capsules, larger seeds, usually denser pu-

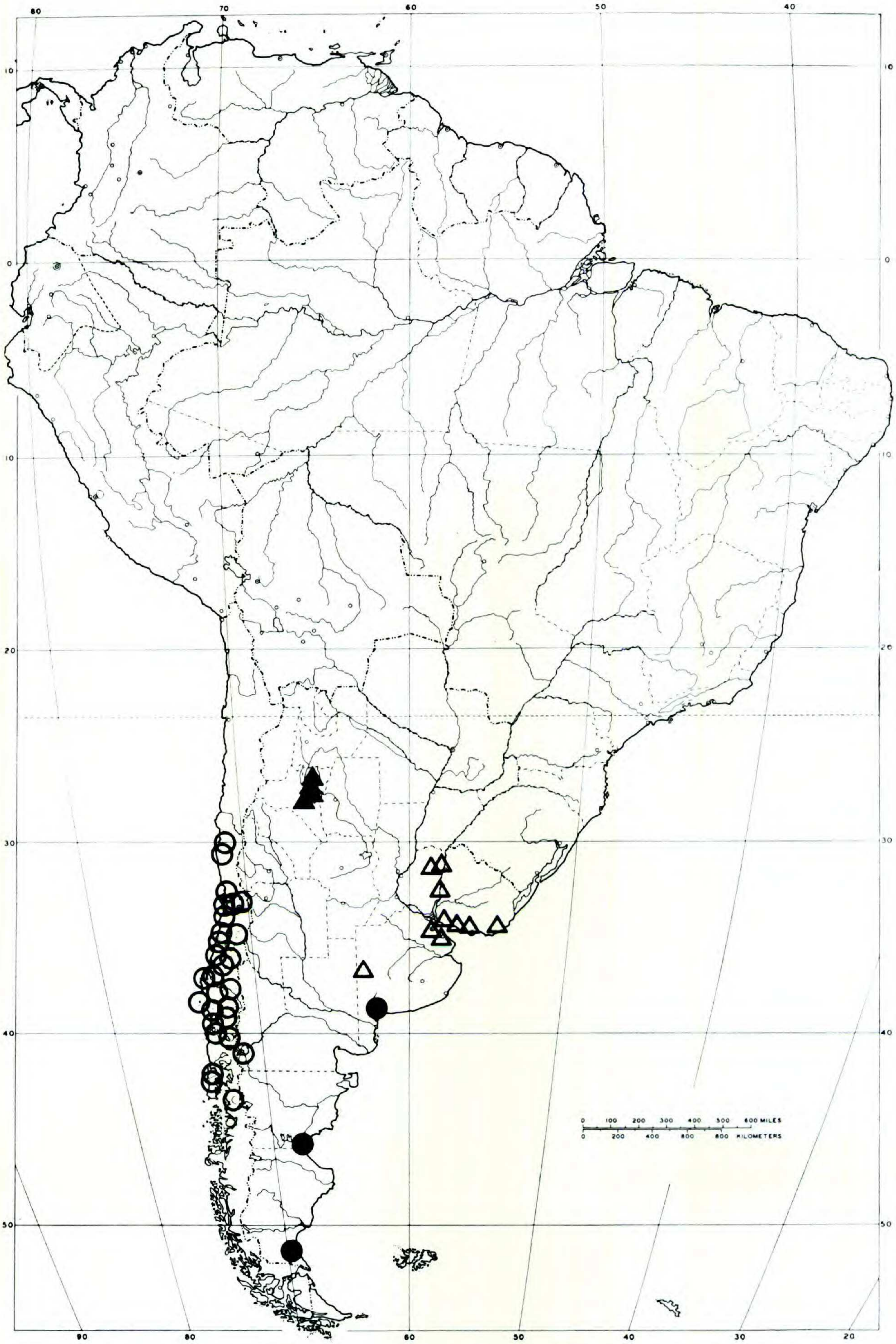


FIGURE 230. Ranges of *Oenothera pedunculifolia* (filled triangles), *O. longiflora* subsp. *longiflora* (hollow triangles), *O. rivadaviae* (dots), and *O. stricta* subsp. *stricta* (circles).

bescence, unflecked sepals, and absence of a rosette. Results from experimental hybridization suggest that one of the genomes of *O. montevidensis* has been derived from *O. indecora* subsp. *indecora*, while the other is an *affinis*-complex derived from *O. mollissima.* All F_1 hybrids between *O. montevidensis* and the chromosomally homozygous *O. indecora* subsp. *indecora* have resembled *O. montevidensis*, but others which were in effect reconstituted *O. indecora* could probably be obtained with further crossing. Similarly, F_1 hybrids with *O. mollissima* all resembled *O. montevidensis.*

27. **Oenothera pseudolongiflora** Dietrich, sp. nov.—FIG. 144.

Herba annua vel biennis, erecta, rosulata, caulis principalis ramosis ramisque arcuate e rosula ascendentibus, 8–15 dm alta. Plantae strigulosae, praecipue ad basin, etiam dense ad sparse pilis longis brevibusque villosis sparseque eis glandulosis praeditae. Folia rosulae anguste oblonga vel angustissime elliptica, acuta, sessilia vel lamina in petiolum gradatim decrescens, 15–20 cm longa, 1.5–2 cm lata; folia caulina anguste oblonga vel angustissime elliptica, acuta, basi acuta vel rotundata, sessilia, 5–10 cm longa, 1–1.8 cm lata; bractea anguste lanceolata vel lanceolata, acuta basi truncata vel subcordata, sessilia, 2–2.5 cm longa, 0.7–1 cm lata, quam capsula subtenta breviora; folia plana, remote obtuseque vel acute serrulata. Inflorescentia ramosa. Tubus floralis 4–6.5 cm longus. Gemmae ambito anguste oblongae vel oblongae, 1.1–1.7 cm longae, 3.5–7 mm crassae, plerumque junctura sepalorum tubo florali rubrofasciatae. Sepala flavo-virescentia; apices sepalorum ca. 1.5 mm longi, erecti. Petala latissime obovata, interdum basi indistincte rubro-maculata, 1.5–2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.5–2 cm longum. Capsula 3–4 cm longa, 3–4 mm crassa. Semina ambito elliptica, 1.1–1.3 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual or biennial herb, forming a rosette, with a branched main stem and side branches arching upward from the rosette, 8–15 dm tall. Plants strigillose, especially near the base, and also densely to sparsely long- and short-villous and sparsely glandular-pubescent. Rosette leaves narrowly oblong to very narrowly elliptic, acute, sessile or gradually narrowed to the petiole, 15–20 cm long, 1.5–2 cm wide; cauline leaves narrowly oblong to very narrowly elliptic, acute, acute to rounded at the base, sessile, 5–10 cm long, 1–1.8 cm wide; bracts narrowly lanceolate to lanceolate, acute, truncate to subcordate at the base, sessile, 2–2.5 cm long, 0.7–1 cm wide, shorter than the capsules they subtend; leaves plane at the margins, remotely serrate, the teeth blunt or sharp. Inflorescence branched. Floral tube 4–6.5 cm long. Buds narrowly oblong to oblong in outline, 1.1–1.7 cm long, 3.5–7 mm thick, usually red striped at the junction of the sepals with the floral tube. Sepals yellowish green; apices of the sepals ca. 1.5 mm long, erect. Petals very broadly obovate, sometimes with an indistinct red spot at the base of each one, 1.5–2 cm long. Anthers 8–10 mm long. Filaments 10–12 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 5–7.5 cm long. Stigma lobes 5–6.5 mm long. Ovary 1.5–2 cm long. Capsule 3–4 cm long, 3–4 mm thick. Seeds elliptic in outline, 1.1–1.3 mm long, 0.5–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–May.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Buenos Aires, sandy soil

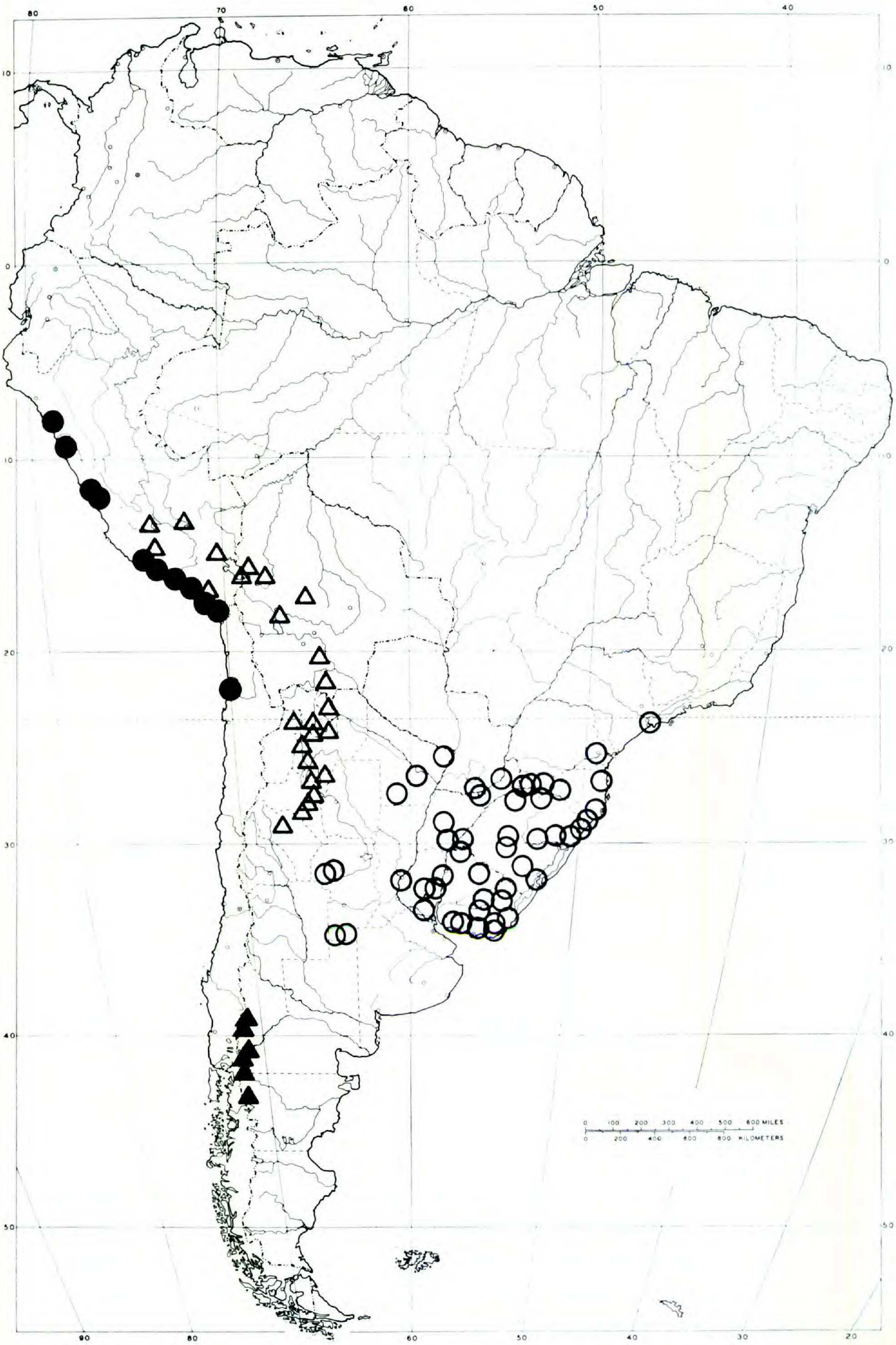


FIGURE 231. Ranges of *Oenothera scabra* (hollow triangles), *O. indecora* subsp. *indecora* (circles), *O. stricta* subsp. *altissima* (filled triangles), and *O. arequipensis* (dots).

at a road on Isla Santiago near La Plata, 5 Jan. 1968, *K. A. Santarius 269* (MO-2155209, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 235): Known only from the region of La Plata, province of Buenos Aires, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Punta Lara near La Plata, *Göpel in 1961** (CTES, DUSS, M, MO). Sandy soil at a road on Isla Santiago near La Plata, *Santarius 269**, *270*, *272*, *274* (DUSS; *269* also M, MO).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: Punta Lara near La Plata, *Rodríguez 520* (LIL); *Rossi 25* (LIL). Isla Paulino, *Cabrera 7384* (GH, LP).

I have named this species *O. pseudolongiflora* because the herbarium specimens I have seen have been determined as *O. longiflora*. The similarity between these two species, however, involves only a general resemblance in habit. As shown by experimental hybridization, *O. pseudolongiflora* has one complex from *O. ravenii*, the second from *O. affinis*. The respective F_1 progenies consisted of two classes of plants, one resembling *O. pseudolongiflora*, the other the second parent. It is interesting that the rosette-forming habit of *O. ravenii* is expressed in *O. pseudolongiflora*, because in the other combinations involving *O. affinis*—*O. picensis*, *O. elongata*, and *O. acuticarpa*—no rosette is formed, just as in *O. affinis*.

In comparison with *O. ravenii*, *O. pseudolongiflora* has smaller flowers and, on the average, a longer floral tube—characteristics that are derived from *O. affinis*. *Oenothera pseudolongiflora* can be distinguished from the two chromosomally heterozygous subspecies of *O. ravenii* by its longer bracts and floral tube. It should not be confused with *O. longiflora* in view of its softer pubescence, in which the long hairs are only 20–30 mμ thick instead of 60–70 mμ as in *O. longiflora*.

Especially in view of its restricted distribution, it appears likely that *O. pseudolongiflora* may be a species of very recent origin.

28. **Oenothera parodiana** Munz, Physis 11: 283. 1933.—FIG. 76–82, 145–148, 223.

Erect or somewhat decumbent annual or biennial herb, forming a rosette, with a simple or branched main stem, the obliquely ascending or arching side branches arising from the rosette, 3–12 dm tall. Plants either exclusively densely strigillose or densely to sparsely strigillose, densely to sparsely long- and short-villous and glandular-pubescent, or densely to sparsely villous and glandular-pubescent. Rosette leaves narrowly oblong to narrowly elliptic or oblanceolate, acute, narrowly cuneate or acute to truncate at the base, sessile or short-petiolate, 10–20 cm long, 0.6–3 cm wide; cauline leaves narrowly oblong to lanceolate or oblanceolate, acute, rounded to truncate at the base, sessile, 2.5–15 cm long, 0.5–2.5 cm wide; bracts oblong to broadly oblong or lanceolate to ovate, acute to obtuse, truncate to subcordate at the base, sessile, 1–2 cm long, 0.5–1 cm wide, shorter than the capsules they subtend; leaves plane or ± evidently undulate at the margins, irregularly or regularly serrate, the teeth sharp or blunt. Inflorescence usually branched. Floral tube 1–4.5 cm long, sometimes flecked and streaked with red. Buds oblong to broadly oblong or broadly elliptic to rotund in outline, green to yellowish green, often flushed with red, often red striped at the junction of the sepals with the floral tube, 0.5–1.5 cm long, 3–5 mm wide. Sepals often flecked with red; apices of the sepals 1–1.5 mm long, erect or divergent. Petals very broadly obovate, rounded or retuse, sometimes with a red basal spot on each one, 0.7–2.5 cm long. Anthers 3–9 mm long. Filaments 5–14 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.8–5 cm long. Stigma lobes 2.5–6 mm long. Ovary 1–2 cm long. Capsule 2–4 cm long, 2.5–5 mm thick, the valves often clearly separated at the end. Seeds elliptic in outline 1.1–1.7 mm long, 0.5–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I). Flowering time: October–May.

Type: Argentina, Prov. Buenos Aires, meadows of El Socorro, Pergamino, 8 Dec. 1926, *L. R. Parodi 7395* (GH, holotype; W, isotype).

Distribution (Figs. 236, 238–239): From the state of São Paulo to Rio Grande do Sul in Brazil; in Uruguay in the departments of Ártigas, Salto, Rivera, Paysandú, Soriano, Colonia, Tacuarembo, Durazno, Cerro Largo, Maldonado, Canelones, Montevideo, Florida, and Flores; in Argentina in the provinces of Misiones, Corrientes, Entre Ríos, Buenos Aires, Formosa, Chacó, Santa Fe, Córdoba, San Luis, La Pampa, Santiago del Estero, and Tucumán.

In an evolutionary sense, *O. parodiana* occupies a position similar to that of *O. sandiana* in series *Renneria*. One might claim, with a certain justification, that *O. parodiana* consists of all the remnants that have not been determined and classified in the series after all of the more clear-cut elements have been taken out. Confronted with the overwhelming diversity of small-flowered phenotypes of this affinity, the taxonomist must of necessity surrender, since the possibility of bringing a neat arrangement out of the group simply does not exist. No fewer than six complexes have participated in the origin of the array of forms here grouped as *O. parodiana*, derived respectively from *O. mendocinensis*, *O. odorata*, *O. ravenii*, *O. longiflora*, *O. indecora*, and *O. affinis*. Except for the local *O. catharinensis* of southern Brazil, these are all of the distinct complexes found in the series *Allochroa*.

From this whole variable array, I have been able to separate only two taxonomically useful entities, *O. parodiana* subsp. *strigulosa* and *O. parodiana* subsp. *brasiliensis*. The first has only strigillose pubescence, and is restricted to the province of Buenos Aires. The second resembles the chromosomally homozygous *O. ravenii* rather closely, but it is small flowered and has longer bracts owing to the influence of *O. affinis* in its genetic constitution. It occurs predominantly in the northeastern and eastern portions of the range of *O. parodiana*.

All other forms have been grouped under *O. parodiana* subsp. *parodiana*. In addition to plants that resemble the type of the species, there are others which almost fall into the range of variation of *O. bahia-blancae*. Still others appear to be very small-flowered plants of *O. picensis* subsp. *cordobensis*. Plants which resemble *O. indecora* closely are not infrequent. Intermediates between the forms that most closely resemble these species and *O. ravenii* frustrate any effort to bring a logical subdivision into play.

There are no internal barriers to interspecific hybridization between the members of series *Allochroa*, and six of the seven available complexes appear to have been recombined in various ways in response to selective pressures to give rise to the array of small-flowered chromosomal heterozygotes grouped under *O. parodiana*. The evolution of self-pollination in these heterozygotes was probably facilitated by its prior existence in the homozygous species *O. mendocinensis* and *O. indecora*. All six of the complexes involved in the assembly of *O. parodiana* are represented together over a broad area in the eastern part of the range of series *Allochroa*.

In addition to uniform populations, there are others which display a great variability. Here and there segregating characteristics such as red flecking on the buds or a red basal spot on the petals crop up and suggest the sort of intermixing which is actively going on at the population level. Since the formation of a ring of 14 is constant in these populations, it can be assumed that a balanced system has evolved within the species whereby combinations of end arrangements leading consistently to this result are continually reformed.

Only a very detailed genetic analysis would lead to a more profound insight into the history of this complex. Such an analysis, if it were carried out, might lead to the taxonomic subdivision of the many forms here grouped under *O. parodiana* subsp. *parodiana*, or even to the recognition of additional species within this group.

KEY TO THE SUBSPECIES

1. Pubescence entirely strigillose .... 28b. subsp. *strigulosa*
1′. Pubescence villous and glandular-pubescent, often also strigillose.
   2. Floral tube 1–2 cm long; petals 0.7–1.2 cm long .... 28a. subsp. *parodiana*
   2′. Floral tube 2.5–4.5 cm long; petals 1.5–2.5 cm long .... 28c. subsp. *brasiliensis*

28a. **Oenothera parodiana** subsp. **parodiana**.—FIGS. 76–82, 145–146, 223.

O. argentinae H. Lév. & Thell. var. *heterotricha* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherlands, Weert, oatfield near the Karelke meal factory, *A. W. Kloos in 1920* (BAS).

Plants erect or somewhat decumbent, 3–7 dm tall. Strigillose, villous and glandular-pubescent, or only villous and glandular-pubescent. Rosette leaves 7–12 cm long, 0.8–1.2 cm wide; cauline leaves 2.5–6 cm long, 0.6–1 cm wide; bracts 1–2 cm long, 0.5–0.8 cm wide; leaves plane or ± evidently undulate at the margins. Floral tube 1–2 cm long. Buds oblong to broadly oblong or elliptic to broadly elliptic, 5–8 mm long, 3–5 mm thick. Petals 0.7–0.2 cm long. Anthers 4–8 mm long. Filaments 6–11 mm long. Style 2–3.5 cm long. Stigma lobes 3–5 mm long. Capsule 2.5–3 cm long, 3.5–3.5 cm thick. Seeds 1.3–1.5 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I).

Distribution (Fig. 238): Found in the departments of Ártigas, Salto, Paysandú, Soriano, Rivera, Tacuarembo, Durazno, Flores, Florida, Canelones, Montevideo, Cerro Largo and Colonia in Uruguay, and in the provinces of Corrientes, Entre Ríos, Santa Fe, Buenos Aires, Córdoba, San Luis, La Pampa, Santiago del Estero, and Tucumán in Argentina.

Specimens examined from cultivated plants:

URUGUAY. COLONIA: Sandy places, port of Juan L. Lacaze, *Santarius 54**, *55**, *56–59*, *60**, *61**, *62*, *63**, *64*, *65*, *66** (DUSS; *55*, *61*, *63*, *66* also CTES; *54*, *55*, *61*, *63*, *66* also M; *54*, *55*, *57*, *61*, *62*, *63*, *65*, *66* also MO). FLORIDA: At the railroad 1 km NE to 3 km SW of Mansavillagra, *Santarius 207**, *210**, *211** (DUSS; *207* also CTES, M; *207*, *211* also MO). 3 km S of Arrayán on Ruta 7, *Santarius 232**, *233*, *235**, *236*, *289–240*, *241** (DUSS; *232*, *235*, *241* also CTES, M; *232*, *236*, *241* also MO). 5 km S, *Santarius 243**, *244–247*, *248**, *249–253* (DUSS; *248* also CTES, M; *243*, *248* also MO).

ARGENTINA. BUENOS AIRES: Stony, grazed hills 2 km W of La Pileta in the Sierra de la Ventana, 350–400 m, *Santarius 468**, *469**, *470**, *471*, *472**, *474*, *479**, *480*, *483*, *485**, *488*, *489* (DUSS; *468*, *469*, *472*, *479*, *485* also CTES; *468*, *469*, *472*, *474*, *479*, *485* also M; *468*, *469*, *472*, *474*, *479*, *483*, *485* also MO). Sierra de la Ventana, rocks and stony hills on both sides of the railroad, 1 km NE of La Pileta, 350 m, *Santarius 494* (CTES, DUSS, M, MO). Sandy places at the coast of Villa del Mar, 5 km NW of Punta Alta, *Santarius 516** (CTES, DUSS, M, MO). Dunes at the road from Villa del Mar to Ruta 229, 5 km NNE of Punta Alta, *Santarius 538**, *541* (DUSS; *538* also MO). TUCUMÁN: Stony places at Río Salí near the bridge of Ruta 9, E of Santa María de Tucumán, 420 m, *Santarius 1655**, *1656** (DUSS; *1655* also M). LA PAMPA: Near La Gloria, *Conrad & Dietrich 57** (DUSS).

Representative specimens examined:

URUGUAY. ÁRTIGAS: *Bartlett 21069* (F, GH, MICH, NY, UC, US). Between Río Uruguay and Arroyo Itacumbú, *Rosengurtt 10510* (MVFA). SALTO: *Felippone 3573* (G). Km 550 at Ruta 3, *Arrillaga 1707* (MVFA). PAYSANDÚ: Ártigas, *Arrillaga 1432* (MVFA). Km 475 at Ruta 3, *Puerto 11305* (MVFA). SORIANO: Est. Media Agua, *Izaguirre 294* (MVFA). Mercedes, *N.N. 181* (POM). COLONIA: Punta Gorda, *Rosengurtt 8639* (MVFA). Riachuelo, *N.N. 9* (BAA). Artilleras, Arroyo de Pintos near Puerto Platero, *Bartlett 20771* (US). RIVERA: Minas de Corrales, *Arrillaga 1221* (MVFA). TACUAREMBO: Valle Edén, *Arrillaga 1733* (MVFA). DURAZNO: Rincón del Bonete, *Arrillaga 1896* (MVFA). FLORES: Río Yi, *Rosengurtt B466* (POM). FLORIDA: Mansavillagra, *Rosengurtt B703* (POM). Arroyo Timote, *Rosengurtt B703* (SI). CANELONES: Arroyo del Saúce, W of Solís, *Bartlett 20968* (GH, MICH, US). Independencia, *Herter 162a* (LIL, SI). MONTEVIDEO: *Isabelle in 1838* (W); *Kuntze in 1892* (CORD); *Bartlett 20681* (MICH, US). Parque Lecoq, *Osorio 669* (LIL). CERRO LARGO: Between Río Negro and Aceguá, *Rosengurtt 851* (POM). Bañado Medina, *Rosengurtt B2518* (GH, LIL, P, POM). Arroyo Malo at Ruta 26, *Lema 7887* (MVFA).

ARGENTINA. CORRIENTES: Santo Tomé, *Pierotti 5571* (LIL). Tabay, *Krapovickas & Cristóbal 13752* (LP). At Ruta 14 near Mercedes, *Cano 1966* (BAB). Dep. Monte Casero, Libertad W of Curuzú, *Ibarrola 2514* (LIL, NY, S). Between Ruta 27 and Río Corrientes near Esquina, *Krapovickas et al. 27112* (CTES, MO). ENTRE RÍOS: Concepción del Uruguay, *Meyer 10437* (LIL). Colón, *Meyer 10565*, *10646*, *10705* (LIL). Concordia, *Burkart 23063* (MO, SI). Río Ceibo, *Burkart 5119* (MO). BUENOS AIRES: Est. Tropezón near 3 de Febrero, *Burkart 4564* (CTES, MO). Bahía San Blas, *Cabrera 4775* (GH, LP, SI). Monte Hermoso, *Carette in 1916* (NY). Casalins, *Fistolera 179* (POM). Libertad near Merlo, *Mazzucconi 669* (BAB). Salalé near Gral. Pintó, *Hicken 4857* (LIL, SI). Castelar, *Lourteig 279*, *360* (LIL). Balcarce, Santa Amarante, *Crovetto 1575* (LIL). Trenque Lauquén, 100 m, *Hunziker 4000* (POM). Elizalde near La Plata, *Dawson 986* (LP). Tandil, *Troncoso in 1937* (K). Junín, *Schulz 5627* (LIL); *Clos 3890*, *3950* (BAB). Tornquist, *Rossi & Bachmann 458* (LIL); *Erettowi 2780* (MO); *Kühnemann 224* (RSA). Pringles, *Osten 143* (BREM). Villa Udaondo, *Vervoorst 5527* (L). SANTA FE: San Cristóbal, *Balegno 591*, *739* (LIL). Km 308 at Ruta 8, between Hughes and Sta. Emilia, *Cano 2784* (BAB). Aurelia near Santa Fe, *Feddersen in 1889* (C). Malabrigo, *Parodi 11222* (POM). Dep. Capital, between Recreo and Loma Río Salado, *Achenbach 421* (SI). CÓRDOBA: San Justo, *Balegno 915* (LIL). Sierra Grande, Cuesta de las Calvas, 1,800 m, *Hunziker 9682* (RSA). Salsipuedes near Colón, *Hunziker 1471* (CORD). Pacheco de Melo near Laboulaye, *Hunziker 12776* (CORD, RSA). Between Mina Clavero and Pampa de Achala, *Di Fulvio 194* (CORD). Road from Tancacha to Río

Tercero, *Scala in 1924* (NY). San Javier, *Castellanos 10731* (RSA). Campino el Cuadrado, *Wall in 1946* (S). Roque Saenz Peña between Laboulaye and Salguero, *Hunziker 12791* (CORD, MO, RSA). Achiras, 800 m, *King 220* (BAB). Huinca Renancó, *King 262a* (BM). Dep. Calamuchita, Athos Pampa, *Hunziker 7087* (UC). SAN LUIS: Cerro Blanco near San Martín, *Hunziker & Cocucci 14657* (CORD). Dique Luján near San Martín, 800 m, *Hunziker & Cocucci 14991* (CORD). LA PAMPA: Catrilo, *Fortuna 57* (LIL, NY, UC). La Gloria, *Fortuna 18* (GH, LIL, NY). Lonquimay, *Fortuna 31* (GH, LIL, NY). Gral. Pico, *Burkart 9913* (LIL, SI). TUCUMÁN: Sierra del Alto, Graneros, road from Catamarca to Tucumán, *Zetarayan 9054* (LIL). Las Cuchillas near Burroyacú, 1,100 m, *Lillo 5319* (LIL). SANTIAGO DEL ESTERO: Ojo de Agua, *Conrad & Dietrich 178* (DUSS).

Specimens from outside of South America:

SOUTH AFRICA. CAPE: Vlottenburg, *Greef in 1969* (K). Dronfield, ca. 9 mi N of Kimberley, ca. 1,300 m, *Leistner 2931* (M). ORANGE FREE STATE: Distr. Glen, *Mostert in 1952* (PRE). LESOTHO: Distr. Tebetebeng, 1957, *Jacot-Guillarmod 2927* (PRE). Distr. Roma, ca. 1,750 m, *Ruch 1586* (PRE). NATAL: Distr. Camperdown, Nagle Dam, ca. 400 m, 1957, *Wells 1146* (PRE). TRANSVAAL: Belfast, 1909, *Leendertz 9202* (PRE). Distr. Potschefstroom, 1948, *Louw 1740* (K, PRE). Distr. Zoutpansberg, farm Rustfontein ca. 9 mi E of Louis Trichardt, 1,300 m, 1955, *Schlieben 7309, 7319* (HBG, K, M). Distr. Pretoria, Queenswood Garden, *Meeuse in 1957* (PRE). Distr. Letaba, ca. 1,020 m, 1958, *Scheepers 270* (M). SOUTH WEST AFRICA: Distr. Windhoek, banks of the White Nossob near farm Bodenhausen, 1961, *Seydel 2686* (GOET, M, MO, SRGH).

RHODESIA. Distr. Lomagundi, Rothwell farm, 1970, *Marc 1087* (K, SRGH). Distr. Salisbury, 1970, *Linky 557* (SRGH). Distr. Melsetter, 1957, *Whellan 1443* (SRGH).

NETHERLANDS. W. Knollendam, near oil refinery "de Vrede," *Kloos in 1920* (L).

GERMANY. Emmerich, oil refinery, *Bonte in 1915* (BAS; as *O. argentinae* H. Lév. & Thell. var. *typica* Kloos & Thell. f. *corynocarpa* Thell.).

FRANCE. Dép. Nord, Dunkerque, *Bouly de Lesdain in 1925* (BAS).

Under this subspecies are grouped all small-flowered complex heterozygotes of series *Allochroa* with varying representation of *O. mendocinensis*, *O. odorata*, *O. ravenii*, *O. longiflora*, and *O. indecora* in their genetic make-up.

28b. **Oenothera parodiana** subsp. **strigulosa** Dietrich, subsp. nov.—FIG. 148.

O. parodiana sensu Munz, Physis 11: 283. 1933, pro parte; Amer. J. Bot. 22: 662. 1935, pro parte.

Plantae erectae, 3–7 dm altae, nonnisi strigulosae. Folia rosulae 7–12 cm longa, 0.6–1 cm lata; folia caulina 4–6 cm longa, 0.5–1 cm lata; bractea 0.9–2 cm longa, 0.5–1 cm lata; folia valde ad margines undulata. Tubus floralis 1.3–2.5 cm longus. Gemmae ambito oblongae vel anguste ovatae, 0.7–1.3 cm longae, 3–4 mm crassae. Petala 1–1.5 cm longa. Capsula 2–3.5 cm longa, 2.5–3.5 mm crassa. Semina 1.2–1.7 mm longa, 0.6–0.8 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants erect, 3–7 dm tall. Plants exclusively strigillose. Rosette leaves 7–12 cm long, 0.6–1 cm wide; cauline leaves 4–6 cm long, 0.5–1 cm wide; bracts 0.9–2 cm long, 0.5–1 cm wide; leaves evidently undulate at the margins. Floral tube 1.3–2.5 cm long. Buds oblong to narrowly ovate in outline, 0.7–1.3 cm long, 3–4 mm thick. Petals 1–1.5 cm long. Anthers 3–5 mm long. Filaments 5–8 mm long. Style 1.8–3 cm long. Stigma lobes 2.5–3 mm long. Capsule 2–3.5 cm long, 2.5–3.5 mm thick. Seeds 1.2–1.7 mm long, 0.6–0.8 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I).

Type: University of California Second Botanical Garden Expedition, 1938–1939, Argentina, Prov. Buenos Aires, 7 km E of Mar de la Plata, sandy soil, exposed high coastal bluffs, in reach of spray, full sun, 50 m, 10 Dec. 1938, *W. J. Eyerdam, A. A. Beetle & E. Grondona 23610* (UC, holotype; GH, K, NA, isotypes).

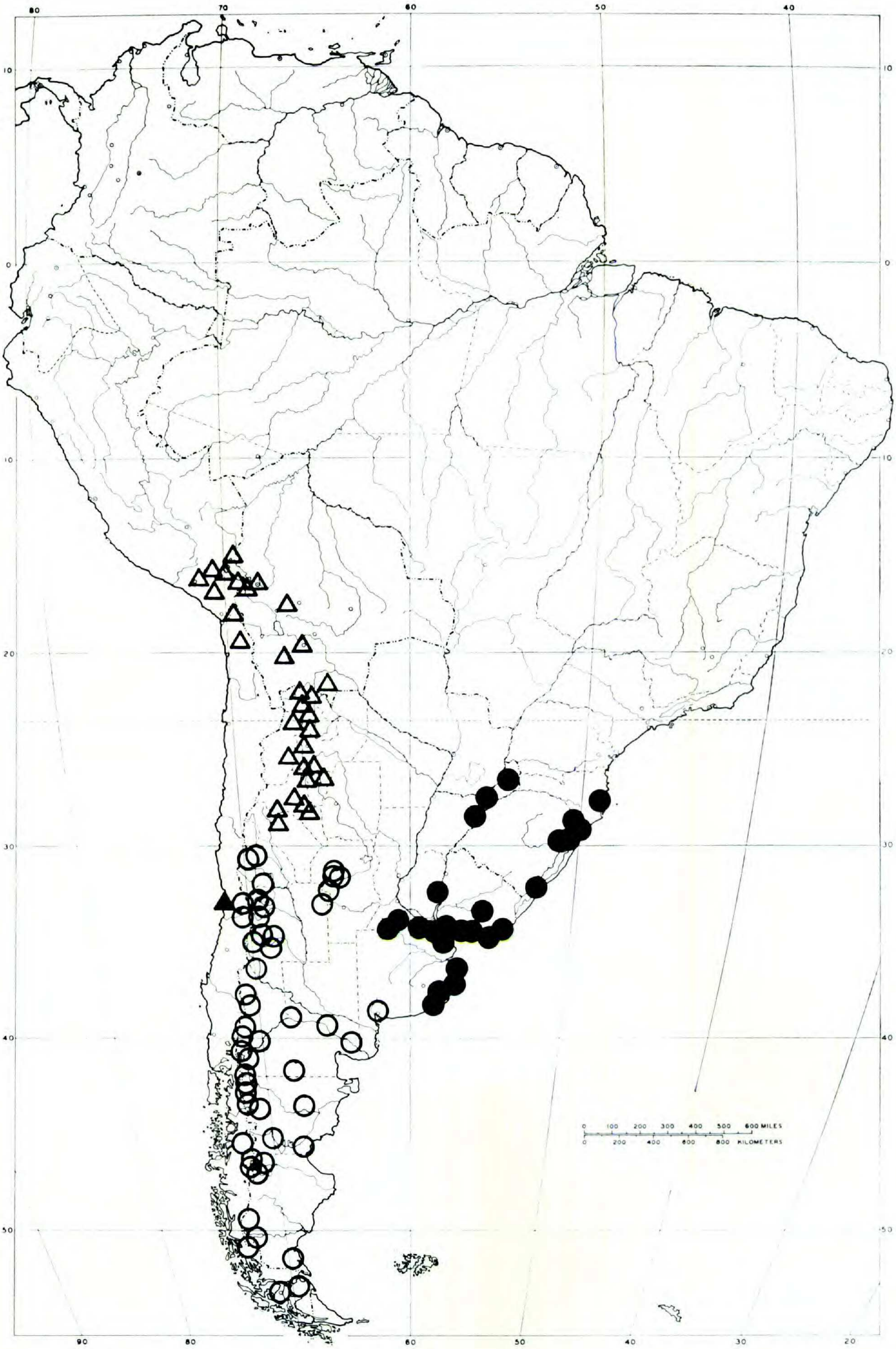


FIGURE 232. Ranges of *Oenothera nana* (hollow triangles), *O. mollissima* (dots), *O. grisea* (filled triangle), and *O. magellanica* (circles).

Distribution (Fig. 239): Only known from the province of Buenos Aires, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Sierra de la Ventana, at the road 2 km W of La Pileta, 300 m, *Santarius 466**, *467* (DUSS).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: *Floyer in 1894* (K). Pergamino, *Parodi 8806* (POM); *Innes in 1914* (K). Bahía San Blas, *Fabris & Schwabe 5012* (LP, RSA). Ituzaingó, *Holmberg 119* (SI). Necochea, *Hicken in 1913* (SI). Trenque Lauquén, 100 m, *Hunziker 4017* (POM). Gral. Pinto, *Hicken 5* (POM). Pila, *León 1901* (BAA). Est. "La Argentina" near Lobería, *Grondona 12957* (BAA). Cerro Redondo near Olavarría, *Krapovickas 3370* (LIL). Sierra de las Tunas, Nuevo Cerro de la Cruz near Cnel. Suárez, *Rossi & Bachmann 464* (LIL). Bahía Blanca, *Soriano 456* (BAB, SI). Sierra La Vigilancia near Balcarce, *Fabris 2614* (CTES, LP). Balcarce, *Crovetto 2487* (BAB). La Copelina between Mar de la Plata and Balcarce, *Spegazzini 89* (BAB). Sierra de Curumalal, *Holmberg 2200* (CORD); *Parodi 10362* (BAA, POM); *Hicken 4* (POM); *Spegazzini 6861* (BAB, POM). Pigué, *Spegazzini 38*, *77* (BAB); *Burkart 4713*, *4794*, *4795* (BAA); *Parodi 10405* (BAA). Est. San Carlos near La Pusana, *Huidobro 1282* (LIL). Cerro La Morediza near Tandil, *Huidobro 1747* (LIL). Gral. Pueyrredón, *Rodríguez 456* (LIL, NY). Punta Mogotes near Gral. Pueyrredón, *Rodríguez 436* (LIL). Sierra de los Padres near Gral. P., *Calderón 543* (MO). Dunes between Mar de la Plata and Miramar, *Hunziker 2202* (SI). Between Asito Unzuá and Parque Camet near Mar de la Plata, *Pelosi 64* (SI). Mar de la Plata, *Hicken 226* (SI), *227* (POM, SI). Sierra la Brava near M. de P., *Hicken 228* (SI). Mar de la Plata, *Valentini 36* (SI); *Bernard 42* (SI); *Carette in 1912* (SI); *Boffa 1* (LP). Gral. Alvaredo, *Crovetto 1498* (BAB, SI). Miramar, *Burkart 17834* (SI, US). Tandil, *Troncoso 1333* (F, LIL, SI); *Krapovickas 2942* (MO, RSA); *Clos 2233* (BAB). Sierra de la Ventana, *Fabris 2692* (LP); *Hicken 4666* (SI); *Boelcke 9587*, *9588* (BAA). Est. Leines, *Alboff 125* (CORD). Cerro Naposta, 300 m, *Gómez 11701* (BAA). Tornquist, *Rossi & Bachmann 462*, *463* (LIL); *Cabrera 4716* (P). La Pileta, *Cabrera 7340* (LP). Los Toldos near Gral. Viamonte, *Crovetto in 1967* (CTES).

Oenothera parodiana subsp. *strigulosa* resembles *O. bahia-blancae*, but is never villous. It has not yet been possible to carry out a program of experimental hybridization to analyze the genetic composition of this subspecies, but on the basis of its characteristics I suspect that *O. mendocinensis*, *O. odorata*, and *O. longiflora* may be involved.

28c. **Oenothera parodiana** subsp. **brasiliensis** Dietrich, subsp. nov.—Fig. 147.

O. parodiana sensu Munz, Physis 11: 283. 1933, pro parte.
Oenothera parodiana "Concordia" Cleland, Jap. J. Genet. 43: 332. 1968.

Plantae erectae, 7–12 dm altae, strigulosae, villosae, et glanduloso-pubescentes. Folia rosulae 8–20 cm longa, 1.2–3 cm lata; folia caulina 5–15 cm longa, 1–2.5 cm lata; bractea 1.5–2 cm longa, 0.7–1 cm lata; folia plana vel valde ad margines undulata. Tubus floralis 2.5–4.5 cm longus. Gemmae ambito anguste oblongae ad oblongas vel lanceolatae ad anguste ovatas, 1–1.5 cm longae, 4–5 mm crassae. Petala 1.5–2 cm longa. Capsula 3–4 cm longa, 3–4(–5) mm crassa. Semina 1.1–1.5 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 7–12 dm tall, erect. Plants strigillose, villous, and glandular-pubescent. Rosette leaves 8–20 cm long, 1.2–3 cm wide; cauline leaves 5–15 cm long, 1–2.5 cm wide; bracts 1.5–2 cm long, 0.7–1 cm wide; leaves plane or evidently undulate at the margins. Floral tube 2.5–4.5 cm long. Buds narrowly oblong to oblong or lanceolate to narrowly ovate in outline, 1–1.5 cm long, 4–5 mm thick. Petals 1.5–2.5 cm long. Anthers 7–9 mm long. Filaments 9–14 mm long. Style 3.5–5 cm long. Stigma lobes 5–6 mm long. Capsule 3–4 cm long, 3–4(–5) mm

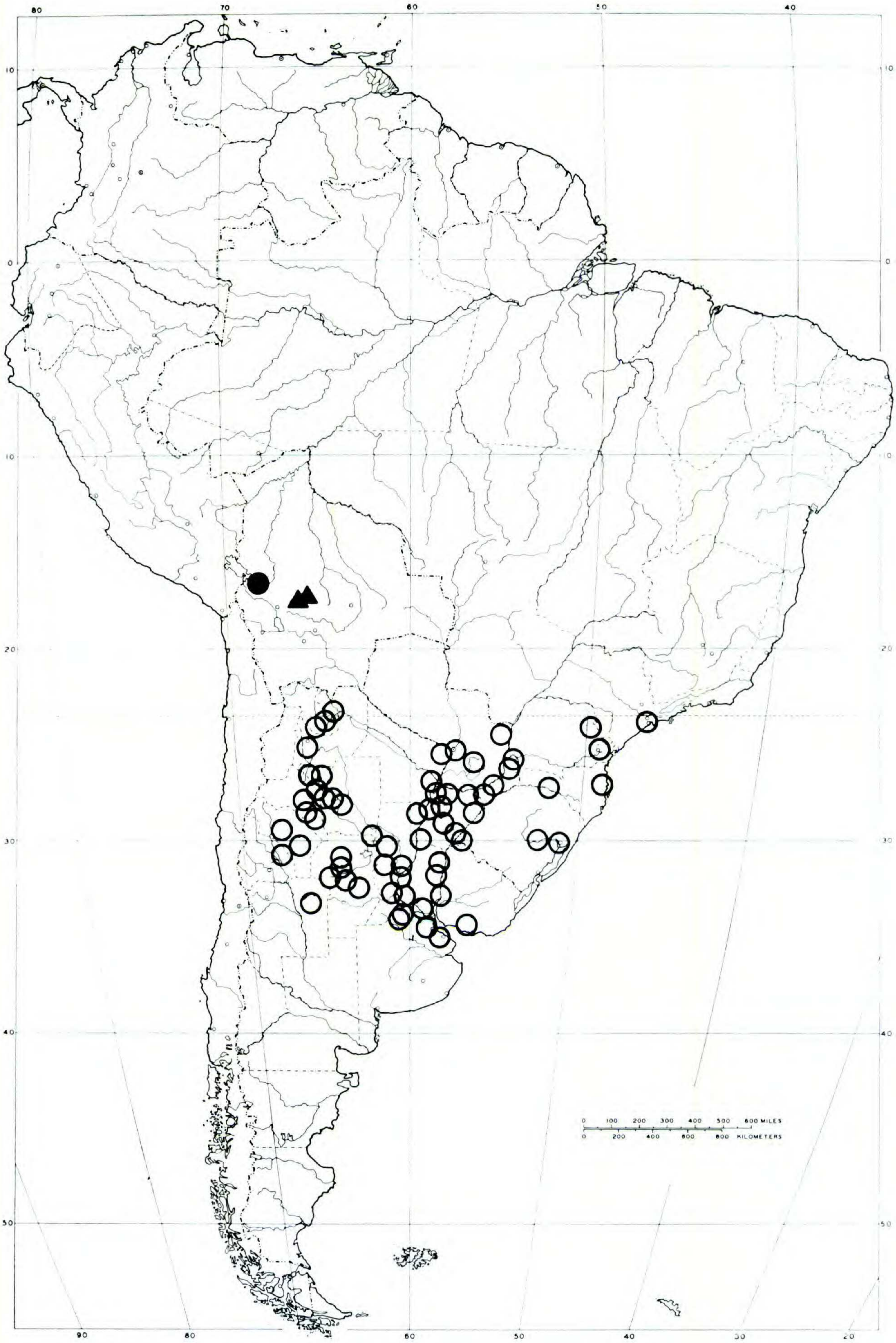


FIGURE 233. Ranges of *Oenothera indecora* subsp. *bonariensis* (circles), *O. indecora* subsp. *boliviensis* (dot), and *O. pseudoelongata* (filled triangles).

thick. Seeds 1.1–1.5 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 11 Aug. 1972. Source: Brazil, Rio Grande do Sul, Pelotas, 1966, _E. J. Hackbart_ (MO-2155412, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 236): From the state of São Paulo to Rio Grande do Sul in Brazil; in the departments of Salto, Rivera, Paysandú, Soriano, Cerro Largo, Maldonado, Montevideo, Canelones, Florida, and Flores in Uruguay; and in the provinces of Misiones, Corrientes, Entre Ríos, Buenos Aires, Formosa, Chaco and Santa Fé in Argentina.

Specimens examined from cultivated plants:

BRAZIL. RIO GRANDE DO SUL: Pelotas, _Hackbart in 1966_ (CTES, DUSS, M, MO), _in 1967_* (CTES, DUSS, M, MO).

URUGUAY. MONTEVIDEO: Carrasco, _Hecht 1964–67_* (CTES, DUSS, M, MO). FLORIDA: _Hecht 1964–31_* (CTES, DUSS, MO).

ARGENTINA. ENTRE RÍOS: Concórdia, _Burkart 23063_* (CTES, DUSS, M, MO, SP). Dep. Concórdia, Ayui, _Burkart 23423_* (DUSS, M, MO). Concepción del Uruguay, _Burkart in 1967_* (CTES, DUSS, M, MO).

Representative specimens examined:

BRAZIL. SÃO PAULO: Jordão, 1,300 m, _Santos_ (R); _Leite 3512_ (GH). SANTA CATARINA: S. Joaquim, 1,300 m, _Reitz & Klein 7977_ (G). Perto de Painel between Lajes and S. Joaquim, 800–1,000 m, _Lutz in 1949_ (R). Campo dos Padres, _Rambo 60069_ (B). RIO GRANDE DO SUL: S. Angelo, _Schwarzer in 1900_ (S). Farroupilha, _Camargo 2636_ (B); _Rambo 40278_ (LIL). Bom Jesus, _Rambo 34863_ (LIL, S). Caxias do Sul, _Sehnem 3994_ (B, SI). Rio Caí near Pôrto Alegre, _Rambo 43868_ (LIL). Caçapava, _Palacios & Cuezzo 1407, 1448_ (LIL). Passo do Socorra near Vacaria, _Rambo 51617_ (S, US). Canôas near Pôrto Alegre, _Palacios & Cuezzo 278_ (LIL). São Leopoldo, _Eugenio 204_ (NY). Bento Gonçalves, _Santos 2616_ (R). Serra dos Taypes, _Schwacke 2597_ (R).

URUGUAY. SALTO: _N.N._ (K). PAYSANDÚ: Km 437 at Ruta 3 near Suelo Chapicuy, _Millot 494_ (MVFA). SORIANO: Est. Mauriño near Mercedes, _N.N. 91_ (POM). RIVERA: Cunapiru, _Wright in 1928_ (BM). FLORES: Between Río Yi and Arroyo Mariacho, _Rosengurtt B1521_ (LIL, POM). FLORIDA: _Rosengurtt B703_ (BAA). Mansavillagra, _Rosengurtt B1657_ (LIL, POM). CANELONES: Dunes near La Floresta, _Steer in 1923_ (HBG). MONTEVIDEO: _Gibert 86a, 341_ (K); _Orbigny in 1829_ (P). Quinta Narelo, _Fruchard in 1876_ (P). Carrasco, _Munz 15451_ (NY, POM). CERRO LARGO: Between Paso Cruz and Río Tacuari, _Arrillaga 2341_ (MVFA). Between Río Negro and Arroyo Aceguá, _Rosengurtt 820_ (POM). MALDONADO: Solís, _Osten 21653_ (BREM); _Cunningham in 1867_ (K).

ARGENTINA. FORMOSA: _Jörgensen 3025_ (POM, SI). CHACO: Las Palmas, _Jörgensen 2487_ (GH, SI, US), _2489_ pro parte (POM). SANTA FÉ: Mocovi, _Venturi 275_ (SI). Chacras between Carcaraña and Cañada de Gomez, _Berndt 5166_ (CORD). Rafaelo near Castellanos, _Terribile 387_ (LIL). MISIONES: Puerto Segundo near Iguazú, _Montes 10363_ (CORD, LP). El Soberbio near Guaraní, _Crisci 297_ (LP). CORRIENTES: Gral. Paz, _Krapovickas & Cristóbal 11836_ (CTES, UC); _Schwarz 321_ (LIL). Dep. Capital, Arroyo Riachuelo at Ruta 12, _Krapovickas & Cristóbal 13783_ (BAA, BAB, C, CTES, LP, MO). La Cruz near San Martín, _Parodi 12368_ (BAA). Juan Pujol near Monte Caseros, _Ibarrola 2323_ (LIL). Est. Tranqueras near Monte Caseros, _Nicora 5187_ (CTES). Vicinity of Concepción, _Ibarrola 022, 431, 546_ (LIL). Vicinity of Paso de los Libres, _Schinini 7699_ (CTES, MO); _Huidobro 3815, 3837_ (LIL). Est. Santa Teresa near Mburucuyá, _Pedersen 93_ pro parte (C). Vicinity of Ituzaingó, _Pierotti 6227, 6195, 6174_ (LIL). Santo Tomé, _Ibarrola 1438_ (LIL, NY); _Krapovickas et al. 21150_ (CTES, MO). Mercedes, _Millan 334_ (POM). Between Ruta 27 and Río Corrientes near Esquina, _Krapovickas et al. 27111_ (CTES, MO). ENTRE RIOS: Villaguay, _Meyer 11187_ (LIL). Colón, _Meyer 10657_ (LIL). Concordia, _Burkart 26731, 28763_ (MO); _Cabrera 19261_ (LP). Concepción del Uruguay, _Lorentz 514_ (BREM, CORD, GOET, K, W). Est. La Selmira near Concordia, _Pedersen 7260_ (C). Federación, _Crovetto 4889_ (BAB). BUENOS AIRES: Est. San Juan, 30 km S of Buenos Aires, _Eyerdam et al. 23037_ (SI). Cajón, _Cabrera 6430_ (LP). Delta del Paraná, Arroyo Carabales, _Burkart 4316_ (CTES).

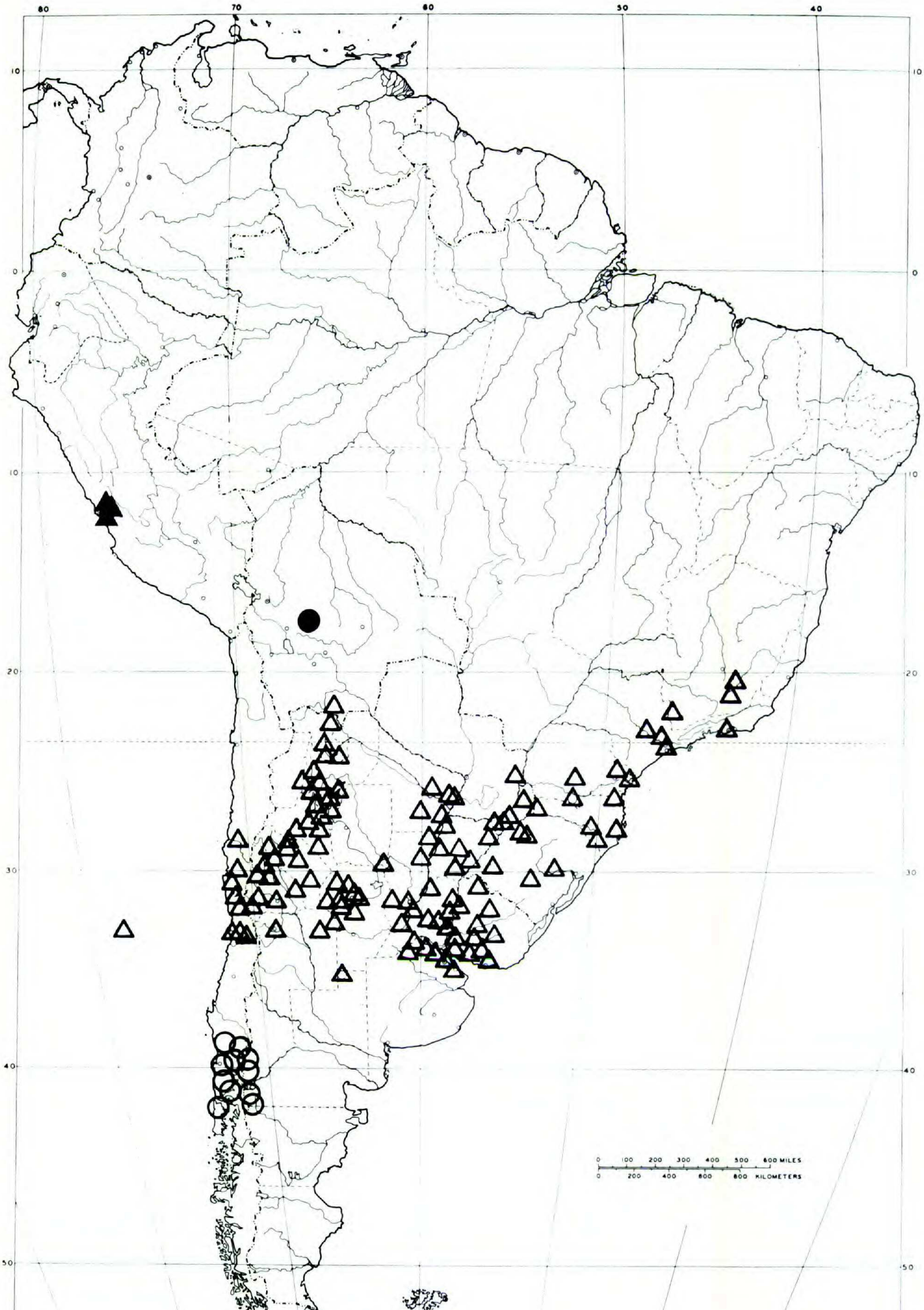


FIGURE 234. Ranges of *Oenothera affinis* (hollow triangles), *O. villaricae* (circles), *O. brevipetala* (dot), and *O. featherstonei* (filled triangles).

In habit, *O. parodiana* subsp. *brasiliensis* resembles the chromosomally homozygous *O. ravenii* very closely. Analysis of the complexes present in this subspecies has shown that it is predominantly derived from *O. ravenii* and *O. indecora*, with some introgression from *O. affinis* and *O. longiflora*, as indicated among other points by the length of the floral tube. Transitional forms with subsp. *parodiana* occur frequently in the zone of contact.

29. **Oenothera verrucosa** Johnston, Contr. Gray Herb. 70: 77. 1924.—FIGS. 12, 149, 185, 209.

Erect annual herb, not forming a rosette, simple or branched from the base upward, 1.5–5 dm tall. Plant moderately to sparsely strigillose, moderately to sparsely villous, and sparsely glandular-pubescent. Cauline leaves very narrowly elliptic to elliptic or lanceolate, acute, attenuate to rounded at the base, only the lowermost short-petiolate, the remainder sessile, 4–8 cm long, 0.5–1.5 cm wide; bracts narrowly lanceolate to lanceolate, acute, rounded to truncate at the base, sessile, 3–5 cm long, 0.5–1.2 cm wide, longer than the capsules they subtend; leaves plane to slightly undulate at the margins, remotely serrulate, the teeth blunt. Inflorescence simple or branched. Floral tube 0.6–1.1 cm long. Buds oblong to broadly elliptic in outline, yellowish, often flushed with red, 0.3–0.6 cm long, 2.5–3.5 mm thick; apices of the sepals 0.5–1 mm long, erect. Petals very broadly obovate, 0.3–1 cm long. Anthers 1–2.5 mm long. Filaments 2.5–4 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 0.8–1.5 cm long. Stigma lobes 1.5–2 mm long. Ovary 0.6–1 cm long. Capsule 1.5–2.5(–3) cm long, 2.5–3.5 mm thick, erect, apparently petiolate; valves spreading apart after dehiscence, not curving. Seeds elliptic in outline, 1.5–1.7 mm long, 0.7–0.8 mm thick, dark brown to almost black. Self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: March–April.

Type: Peru, Dep. Arequipa, ravines and rocky slopes, Pampa, southern slopes of Chachaní Mountain north of Arequipa, 3,660 m, Mar. 1920, *Mr. and Mrs. F. E. Hinkley 17* (GH, holotype; BAS, isotype).

Distribution (Fig. 238): Known only from the Andes of the department of Arequipa, southern Peru, at elevations from 2,400–3,700 m.

Specimens examined from cultivated plants:

PERU. Dep. Arequipa: Quebrada de San Lázaro, 5–6 km NNE of Arequipa below the El Misti, sandy places W of the river, 2,600 m, *Santarius 2068**, *2071*, *2073** (DUSS; *2068*, *2073* also M; *2068* also CTES, MO).

Additional specimens examined:

PERU. AREQUIPA: Near Arequipa, *Stafford D10* (K); 2,700 m, *N.N. in 1954* (RSA); 2,400–2,600 m, *Pennell 13174* (F, GH, K, NY, S, US, USM); *Nuñez 97* (USM); *N.N. in 1925* (US-1231003). Baño de Jesus, 2,600–2,700 m, *Ferreyra 14252* (USM). Slopes of the Misti between Yura and Arequipa, *Sandeman 3960* (K). Mountains near Yura, 2,575–2,600 m, *Vargas 7974* (LIL, MO, RSA). Quebrada San Lázaro, 2,800 m, *Munz 15483*, *15527*, *15528* (POM). Chihuata 20 km E of Arequipa, 2,600 m, *Munz 15540* (POM, US). Characato near Arequipa, 2,400–2,600 m, *Vargas 8043* (LIL).

Oenothera verrucosa seems to be a declining species which has found a last refuge in the Andes of Arequipa. It evidently participated in the origin of the derivative complex heterozygote *O. arequipensis*, which occurs at low elevations along the coast of southern Peru and northern Chile. Possibly *O. verrucosa* at one time occupied much of the same area as *O. arequipensis*, but more likely that derivative species was simply able to expand its range into the newly developed very arid regions during and after the Pleistocene, whereas *O. verrucosa* became confined to its present very limited area of distribution.

An important characteristic of *O. verrucosa* is the stipitate appearance of its erect capsules, owing to their abrupt narrowing toward the base. *Oenothera verrucosa* and the following two species, *O. coquimbensis* and *O. arequipensis*, are obligate annuals and do not form a rosette. Responding to the short period of growth available to them, they elongate rapidly after forming only a few leaves and form their first buds only 4–5 weeks after germination. In cultivation, all other species require a much longer time for the initiation of their first buds.

30. **Oenothera coquimbensis** Gay, Fl. Chil. 2: 331. 1847.—FIGS. 150–151, 186.

O. grandidentata Philippi, Linnaea 33: 68. 1864. LECTOTYPE: Chile, Prov. Atacama, near Caldera, Dec. 1854, *R. A. Philippi* (SGO-052835, GH, NY and POM photographs); Munz, Amer. J. Bot. 22: 658. 1935.

O. coquimbensis Gay var. *grandidentata* (Philippi) Reiche, Anales Univ. Chile 98: 476. 1897; Fl. Chile: 258. 1898.

Onothera albicaulis Pursh var. *tigrina* H. Lév. subvar. *coquimbensis* (Gay) H. Lév., Monogr. Onoth. 345. 1909; Bull. Acad. Int. Géogr. Bot. 19: 305. 1909.

Raimannia coquimbensis (Gay) Sprague & Riley, Bull. Misc. Infor. 1921: 200. 1921.

Erect annual herb, not forming a rosette, simple or branched from the ground upward, 0.5–5 dm tall. Plants densely to moderately strigillose, moderately long- and short-villous. Cauline leaves very narrowly elliptic to elliptic or lanceolate to narrowly ovate, acute, acute to truncate at the base, sessile, 5–8 cm long, 0.5–1.5 cm wide; bracts narrowly lanceolate to narrowly ovate, acute, truncate to subcordate at the base, subsessile, 2–6 cm long, 0.5–1.5 cm wide; leaves usually plane at the margins, irregularly and coarsely toothed or ± regularly and deeply toothed, sometimes doubly so, often flecked with dark reddish brown. Inflorescence simple or branched. Floral tube 1–3 cm long. Buds broadly elliptic to narrowly ovate in outline, yellowish, often striped with red at the junction of the sepals with the floral tube, 0.5–1.3 cm long, 3–3.5 mm thick; apices of the sepals 1–3 mm long, erect or divergent. Petals very broadly obovate, 0.8–2 cm long. Anthers 2.5–6 mm long. Filaments 5–13 mm long. Style held above the anthers in most individuals, occasionally shorter and then the anthers shedding directly on it at anthesis, 2–4 cm long. Stigma lobes 2.5–4 mm long. Ovary ca. 1 cm long. Capsule 1–2.5 cm long, 2.5–3.5 mm thick, ± erect or spreading obliquely from the stem, often somewhat enveloped by the subtending bract. Seeds narrowly elliptic in outline, 1.2–1.6 mm long, 0.4–0.5 mm thick. Self-compatible but mostly outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: September–November.

Type: Chile, Prov. Coquimbo, on dunes at the edge of the sea, very rare, vicinity of La Serena, Dec. 1836, *Cl. Gay 520* (P, holotype; F, GH, K, P, isotypes).

Distribution (Fig. 239): Sandy flats and dunes near the coast in the semideserts of Chile from Antofagasta to Purén, Malleco Province.

Specimens examined from cultivated plants:

Grown from seeds of a herbarium specimen in 1973 at MO. Source: Chile, Prov. Atacama, Dep. Freirina, road from Chañaral de Aceituna to Bahía Carrizal at km 6, *Marticorena, Rodríguez, Weldt 1846** (CONC-36723).

Additional specimens examined:

CHILE. ANTOFAGASTA: Base of hills just SE of La Chimba, *Johnston 3640* (GH, US). ATACAMA: *Geisse in 1885–1887* (NY); *Morong 1141, 1162, 1231, 1264* (NY), *1285* (K, MICH, NY, US). Chañaral, *Ricardi 2258* (CONC). Hills back of El Barquito at Puerto de Chañaral, *Johnston 4772* (CH). Vicinity of Caleta Pan de Azúcar, dunes on point just S of the Caleta, *Johnston 5839* (F, GH, K, LIL, S, US). Road from Chañaral de Aceituna to Bahía Carrizal at km 6, *Marticorena 1846* (CONC). Carrizal, *N.N. in 1885* (SGO-052891). Huasco, *Monypenny 46* (CONC). Algarrobal at Pan-Amer. Highway, *Cabrera 12649* (LP). *Ricardi 4410-795* (CONC). 1 km S of Huasco, *Böcher et al. 540* (C). Vicinity of Copiapó, 370 m, *Johnston 4990, 5030* (GH); *Philippi 1726* (SGO); *N.N. in 1885* (SGO-052892). Pan-Amer. Highway between Caldera and Chañaral at km 18, *Ricardi et al. 1304-B* (CONC). Between Copiapó and Vallenar at km 55, *Ricardi et al. 1511* (CONC). At km 40, *Ricardi 2210* (CONC). Morro de Copiapó, sandy washes along a stream near the sea, *Worth 16185* (K, UC). Quebrada de Chanchoquin near Copiapó, *Gigoux in 1895* (GH). Travesia, *Kohler 153* (CONC); *Jiles 2160* (CONC); *N.N.* (SGO-052890). Caldera near Copiapó, *Gigoux in 1894* (GH); *Philippi 1726b, 1726c, 1724* (SGO), *in 1885* (SGO-052889). Piedra Colgada, *Philippi in 1885* (SGO-052893, SGO-052887). Bandumias, *Geisse 1726a* (SGO). Pojonales, *Geisse in 1888* (SGO). COQUIMBO: *Gay in 1838* (P); *Reiche in 1909* (SGO-052879); *Jaffuel 2679* (GH); *Philippi 785* (US); *Elliott 85* (K). Between La Serena and Punta de Teatinos, *West 3919* (GH, MO, UC). La Serena, Choros Bajos, *Marticorena 1694* (CONC). Between Herradura and Coquimbo, *Skottsberg in 1917* (NY, S). Dunes between Tongoy and Guanaqueros near Ovalle, *Gleisner 5* (CONC). Est. Talca near the sea, dep. Ovalle, *Jiles 1425* (CONC, S). Quilimarí, *in 1862* (SGO-052833). VALPARAÍSO: Valparaíso, *Calvert in 1914* (BM). MALLECO: Near Purén, *N.N. 1229 in 1838* (SGO-052834).

Cultivated specimens:

Botanical Garden, Leningrad, seeds from Chile, Prov. Atacama, from sandy plains near Huasco, sent by Cuming, *in 1847* (LE; as *O. glauco-virens* F.M.).

Oenothera coquimbensis is totally distinct from *O. verrucosa* in its characteristic pattern of toothing of the leaves, its larger flowers, and its different mode of capsular dehiscence, in which the valves curve inward. In addition, the capsules usually spread obliquely from the stems instead of standing erect and are often partially enfolded by their subtending bract. Finally, the seeds are shorter and narrower than those of *O. verrucosa*.

Within *O. coquimbensis* there are two distinctive variants, but these are so completely joined by intermediate forms that it does not seem desirable to accord them formal taxonomic recognition. One has extraordinarily deeply toothed leaves in which the teeth are very narrow and long and often also secondarily toothed. The second has relatively wide leaves which are merely coarsely serrate.

Oenothera coquimbensis, *O. arequipensis*, and to some extent, *O. nocturna*, species of the coastal deserts of Peru and Chile, appear only in years of ample rainfall, and thus represent a distinctive ecological type within subsect. *Munzia*. The evolution of these deserts, and consequently of the species that inhabit them, is a phenomenon of Late Pleistocene and Recent time (Raven & Axelrod, 1974).

31. **Oenothera arequipensis** Munz & Johnston, Contr. Gray Herb. 75: 20. 1925. —FIGS. 152, 187–188.

O. laciniata Hill var. *limensis* Munz & Johnston, Contr. Gray Herb. 75: 20. 1925. TYPE: Peru, Dep. Lima, sandy lomas along the sea near Lurín, 23 Sep. 1925, *J. F. Macbride 5950* (F-536954, holotype, NY, photograph; GH, K, US isotypes).
O. laciniata var. *nocturna* (Jacq.) Munz, Amer. J. Bot. 22: 656. 1935, pro parte.
O. laciniata sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 537. 1941, pro parte.
O. verrucosa sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 540. 1941, pro parte.

Erect annual herb, not forming a rosette, usually branched near the base, 1–3.5 dm tall. Plant densely to sparsely strigillose and densely to sparsely appressed- or erect-villous, sometimes almost glabrous. Cauline leaves narrowly elliptic to narrowly oblanceolate, acute, gradually narrowed to the short petiole, 2–10 cm long, 0.5–2 cm wide; bracts narrowly elliptic to narrowly ovate, acute, acute at the base, sessile, 2.5–5 cm long, 0.5–1.5 cm wide, longer than the capsules they subtend; leaves plane to slightly undulate at the margins, usually deeply sinuate. Inflorescence usually branched. Floral tube 1–3 cm long. Buds oblong in outline, yellowish, sometimes flushed with red, 0.3–0.8 cm long, 2–4 mm thick; apices of the sepals 1–2 mm long, erect or divergent. Petals very broadly obovate, 0.4–1.5 cm long. Anthers 2–3.5 mm long. Filaments 5–7 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.3–4 cm long. Stigma lobes 2–3.5 mm long. Ovary ca. 1 cm long. Capsule 1.5–3 cm long, 2.5–4 mm thick, tapering at both ends and usually appearing pedicellate, mostly erect; valves spreading apart in dehiscence. Seeds elliptic to nearly rotund in outline, 1–1.3 mm long, 0.6–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: September–November.

Type: Peru, Dep. Arequipa, sandy slope, desert hills near Mollendo, 17 Nov. 1923, A. S. *Hitchcock 22403* (US-1,196.655).

Distribution (Fig. 231): In the lomas of the Pacific coastal deserts and semideserts of Peru from the department of Libertad to Tacna, ascending to 2,700 m elevation in the vicinity of Lima; in Chile only known from Tocopilla in the province of Antofagasta.

Specimen examined from cultivated plants:

PERU. LIMA: Prov. Huarochirí, Huascamarca near Santiago de Tuna, 2,700 m, *Encarnación* 346* (DUSS).

Additional specimens examined:

PERU. LA LIBERTAD: Cerro Campana near Trujillo, 350 m, *López 0907* (US). Cerro Cabezon near Trujillo, 400–500 m, *Weberbauer in 1940* (USM). ANCASH: Lomas de Casma near Santa, 250–300 m, *Ferreyra 8039* (US). LIMA: Lima, *Cuming 1079* (K); *Soukup 2158* (F); *Mathews* pro parte (K). Lomas near Barranco, 50–100 m, *Weberbauer 5703* (F, GH, US). San Agustín, *Asplund in 1940* (RSA). Lomas de Atocongo, 300–400 m, *Ferreyra 2448* (US). Lomas de Lachay near Chancay, *Cerrata 3825* (MO). Pasomayo near Chancay, 300 m, *Stork 9353* (GH, K, UC). Hacienda Desagravio near Huaura, *Goytizolo in 1943* (USM-12875). AREQUIPA: Arequipa, *in 1892* (GH). Mollendo near Islay, 300 m, *Ferreyra 12102* (USM); *Mexia 04167* (MO, UC, US); *Stafford 279* (K). Hillside directly back of the port, *Johnston 3556, 6303* (GH); *Worth & Morrison 15764* (GH, K, UC). Slopes of the Misti, *Cárdenas & Rodríguez 3* (F). Prov. Caravelí, Lomas de Jahuay, km 534 between Nazca and Chala, 300–400 m, *Ferreyra 1396* (USM). Lomas de Capac near Chala, 300 m, *Ferreyra 1433* (USM). Between Tambo and Posco, 300–550 m, *princess Therese of Bavaria 233* (M). Lomas de Camaná, 600–700 m, *Ferreyra 6440* (US, USM). Cerro los Cerillos, W of Pan Am. High-

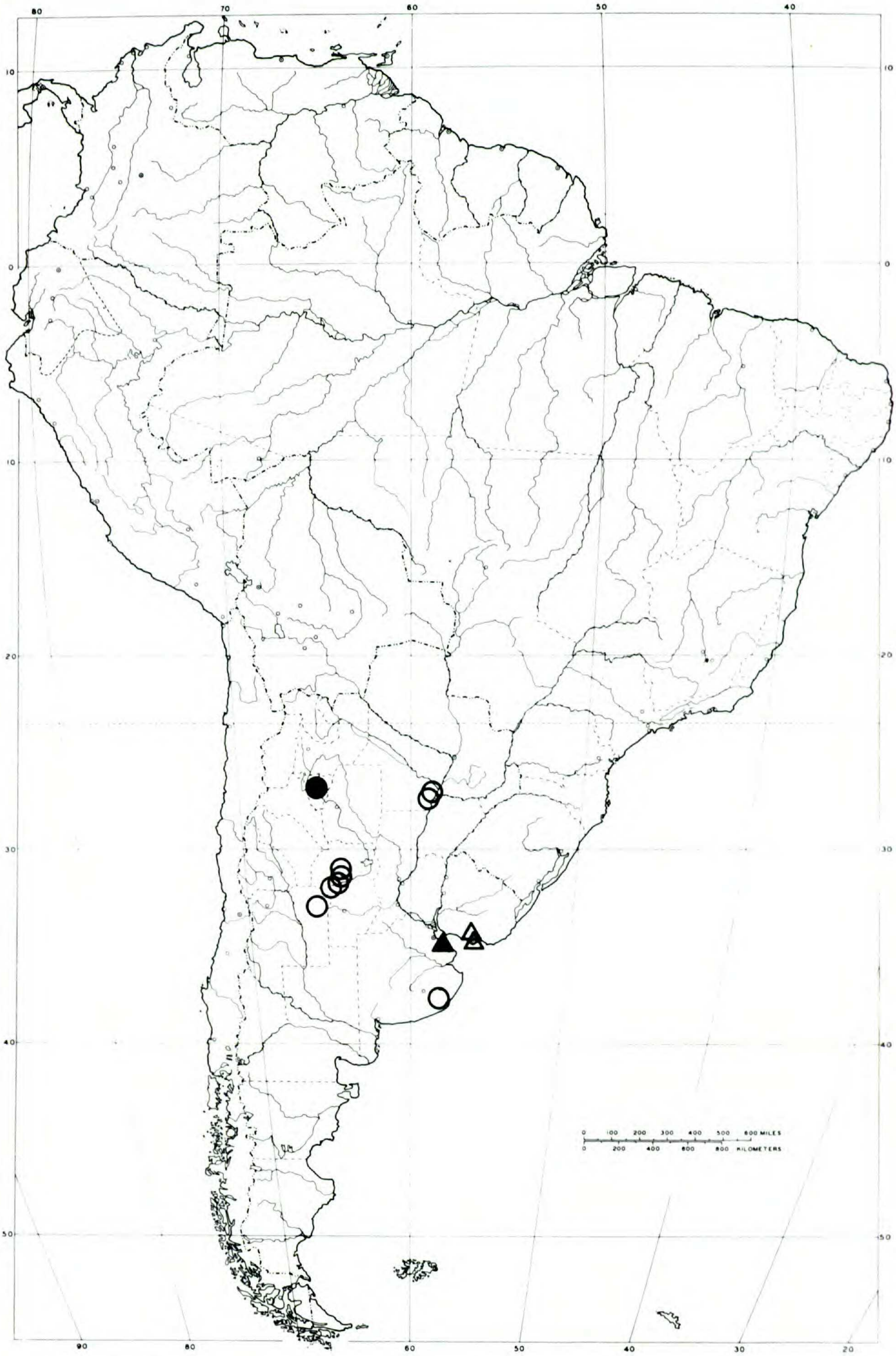


FIGURE 235. Ranges of *Oenothera stricta* subsp. *argentinae* (circles), *O. montevidensis* (hollow triangles), *O. pseudolongiflora* (filled triangle), and *O. hechtii* (dot).

way, 52 km S of Nazca, km 500, 650 m, *Rahn 130* (C). Along Pan-Amer. Highway, 28.9 km NW of Chala, 240 m, *Rahn in 1957* (C). Capac, *Scolnik 1019* (CORD, LIL, RSA). MOQUEGUA: Lomas de Ilo near Mariscal Nieto, 600–700 m, *Ferreyra 12577* (BM, MO, USM). Lomas de Mostacilla near Ilo, 300 m, *Vargas 8598* (LIL). TACNA: Morro de Sama, 450 m, *Delarte 7315* (RSA).

CHILE. ANTOFAGASTA: Dep. Tocopilla, steep hillside ca. 6 km north of port and about opposite Caleta Duendes, *Johnston 3602* (GH, S, US). Tocopilla, *Jaffuel 2554* (GH).

The close similarity in general aspect between *O. arequipensis* and *O. verrucosa* led Munz (1935) to combine them as a single species ten years after first describing the former. Notwithstanding this, there are fundamental differences between them. *Oenothera arequipensis* is branched to a greater extent and has sinuate leaves and seeds that are much broader. Moreover, *O. verrucosa* is chromosomally homozygous and occurs only at elevations greater than 2,000 m in the department of Arequipa; *O. arequipensis* is a complex heterozygote and inhabits mainly the sea-level lomas of the coastal deserts of Peru and northernmost Chile.

No hybrids involving *O. arequipensis* have yet been analyzed to determine the genomes involved in the formation of this species. Nevertheless, it probably contains a genome derived from *O. verrucosa*, since the resemblance between these two species is much too close to be attributed to chance. Its second genome is probably derived from *O. laciniata* subsp. *pubescens*, which ranges south at least to the Peruvian Departments of Lima and Junín. At the very least, the second genome of *O. arequipensis* must contain a strong admixture of genes from this entity, as indicated by the sinuate leaves and the seeds which are often nearly rotund in outline. On the other hand, *O. arequipensis* never exhibits the nodding buds of *O. laciniata*.

Oenothera arequipensis provides an impressive example of the reticulate relationships between the subsections of sect. *Oenothera*, linking a highly derived South American species with a "late arrival" in South America as a complex heterozygote of rather local distribution in a habitat that is clearly marginal for the genus as a whole.

32. **Oenothera grisea** Dietrich, sp. nov.—FIGS. 86–87, 154.

Herba annua erecta, non rosulata, multiramosa, 2–5 dm alta, nonnisi denseque strigulosa, caulibus foliisque ut videtur griseo-viridibus. Folia caulina anguste elliptica vel anguste lanceolata, acuta, basi acuta vel rotundata, sessilia, 5–10 cm longa, 0.8–1.2 cm lata; bractea lanceolata vel ovata, acuta, basi truncata vel subcordata, sessilia, 2–3 cm longa, 1–1.5 cm lata; folia manifeste ad margines undulata, irregulariter obtuseque serrata. Inflorescentia ramosa. Tubus floralis 1–1.5 cm longus. Gemmae ambito oblongae vel ellipticae, 0.8–1 cm longae, 3–4 mm crassae, griseo-virides; apices sepalorum 1–1.5 mm longi, divergentes. Petala latissime obovata, 0.8–1.2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 6–7 mm longum. Capsula 2–2.5 cm longa, 2.5–3.5 cm crassa. Semina ambito elliptica, 1.3–1.5 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, usually with many branches arising from the base upward, 2–5 dm tall. Plants exclusively and densely strigillose, the stems and leaves appearing gray green. Cauline leaves narrowly elliptic to narrowly lanceolate, acute, acute to rounded at the base, sessile, 5–10 cm long, 0.8–1.2 cm wide; bracts lanceolate to ovate, acute, truncate to subcordate at the base, sessile, 2–3 cm long, 1–1.5 cm wide; leaves evidently undulate along the margins, irregularly serrate with blunt teeth. Inflorescence branched. Floral tube 1–1.5 cm long. Buds oblong to elliptic in outline, 0.8–1 cm long, 3–4 mm thick, gray green; apices of the sepals 1–1.5 mm long, divergent. Petals very broadly obovate, 0.8–1.2 cm long. Anthers ca. 4 mm long. Filaments 5–6 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.5–2.5 cm long. Stigma lobes ca. 3 mm long. Ovary 6–7 mm long. Capsule 2–2.5 cm long, 2.5–3.5 cm thick. Seeds elliptic in outline, 1.3–1.5 mm long, 0.5–0.7 mm thick, brown. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: December–March.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 17 Aug. 1971. Source: Chile, Prov. Valparaíso, Las Ventanas, end of 1965, *L. Constance* (MO-2155203, holotype; DUSS, M, isotypes).

Distribution (Fig. 232): Known only from the dunes at Concón, province of Valparaíso, Chile.

Specimens examined from cultivated plants:
CHILE. VALPARAÍSO: Las Ventanas, *Constance in 1965** (DUSS, M, MO).
Additional specimens examined:
CHILE. VALPARAÍSO: Ritoque, dunes near Concón, *Poulson in 1952* (C). Quinteros near Concón, *Philippi in 1866* (W). Dunes near Concón, *Jaffuel 3956* (GH); *Zöllner 6086* (L).

The complex heterozygote *O. grisea* is similar in habit to *O. coquimbensis*, but can be distinguished by its exclusively strigillose pubescence; plants of *O. grisea* are grayish in appearance. This species grows poorly in cultivation, and the flowers often drop off prematurely or do not form any pollen. For this reason, it has not yet been possible to analyze its genetic constitution fully. However, one genome seems to have been derived from the *odorata*-complex of *O. stricta* because hybridization with *O. odorata* produces an F_1 generation in which one type is very similar to *O. odorata*. The second genome may have been derived from the chromosomally homozygous *O. coquimbensis*, as suggested by the morphological similarity between that species and *O. grisea*. Both of the putative parents, *O. coquimbensis* and *O. stricta*, grow in the same area as *O. grisea*. The restricted distribution of *O. grisea*, which occurs only on the dunes at Concón near Valparaíso, seems to indicate a very recent origin for this species.

33. **Oenothera featherstonei** Munz & Johnston, Contr. Gray Herb. 75: 19. 1925. —FIGS. 153, 189.

Erect annual or perhaps sometimes perennial herb with arcuate side branches, to 5 dm tall. Plants exclusively strigillose. Cauline leaves very narrowly elliptic to elliptic, acute, narrowly cuneate at the base, short-petiolate, 3–5 dm long, 0.8–1.2 cm wide; bracts narrowly elliptic to lanceolate, acute, attenuate at the base, 2.5–4 cm long, 0.5–1 cm wide; leaves plane at the margins, irregularly serrate, the teeth sharp or blunt. Inflorescence branched. Floral tube 3–4 cm long. Buds lanceolate in outline, 2–3 cm long, 5–9 mm thick, yellowish;

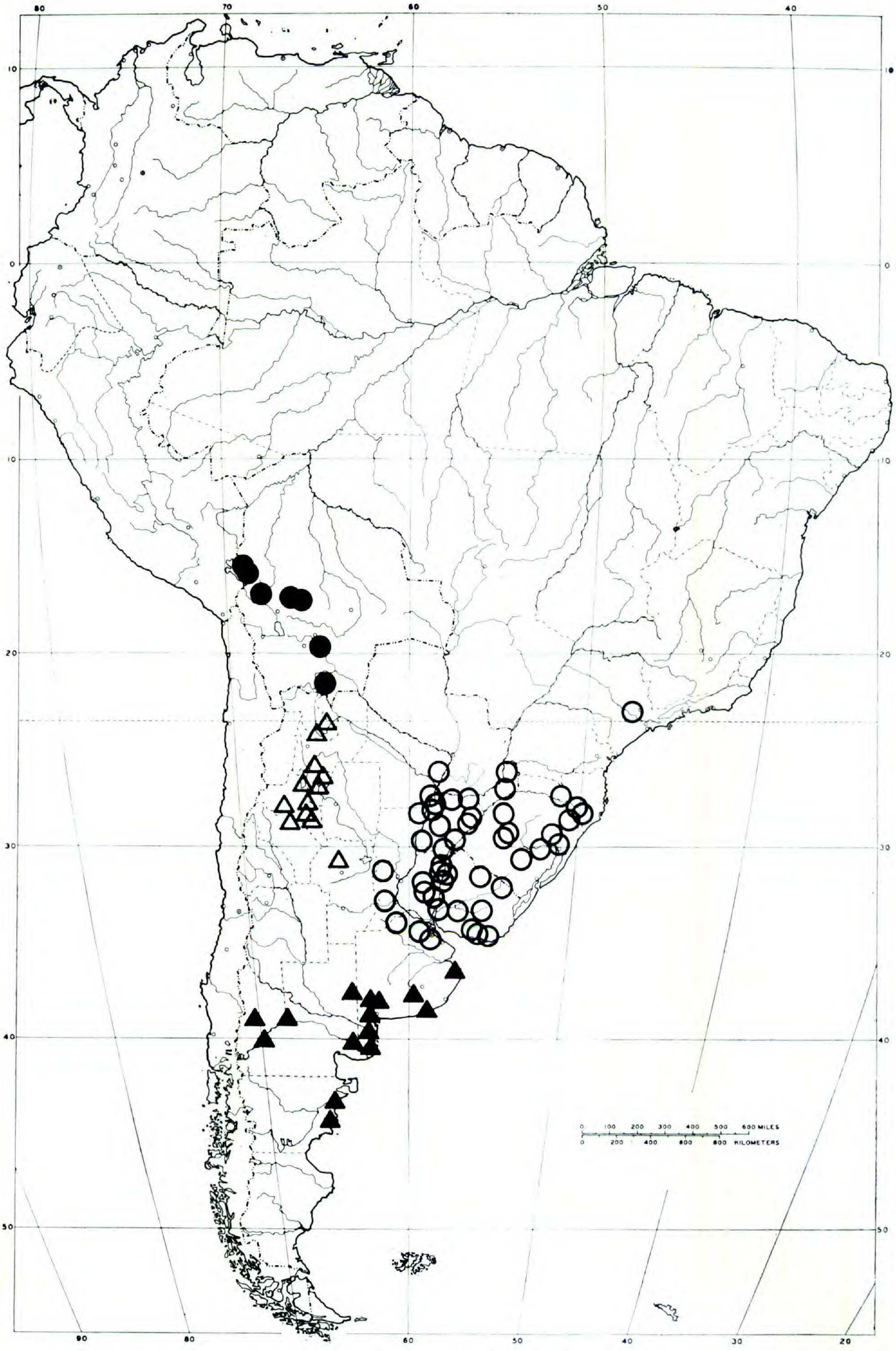


FIGURE 236. Ranges of *Oenothera bahia-blancae* (filled triangles), *O. parodiana* subsp. *brasiliensis* (circles), *O. elongata* (dots), and *O. tucumanensis* (hollow triangles).

apices of the sepals 2–4 mm long, divergent. Petals very broadly obovate, 2.5–4 cm long. Anthers 8–12 mm long. Filaments 16–24 mm long. Style long, the stigma elevated well above the anthers at anthesis, 4–7.5 cm long. Stigma lobes 3–7 mm long. Ovary 1.5–2 cm long. Capsule 2–2.5 cm long, 2.5–3 mm thick. Seeds elliptic in outline, 1.3–1.5 mm long, 0.6–0.7 mm thick, dark brown to almost black. Self-compatible but outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 8 and 3 bivalents** or ring of 10 and 2 bivalents*** at meiotic metaphase I). Flowering time: February–May.

Type: Peru, Dep. Lima, sprawling on disintegrated granite slope, Matucana, 12 Apr.–3 May 1922, *J. F. Macbride & Featherstone 270* (F-516,803, NY photograph; G, GH, K, isotypes).

Distribution (Fig. 234): Apparently only in the vicinity of Matucana, department of Lima, Peru, at elevations of 2,000–2,500 m.

Specimens examined from cultivated plants:

PERU. LIMA: Prov. Huarochirí, at km 63 of the railroad from Lima to Oroya, between Surco and Puente Quitasombrero, 2,050–2,100 m, *Encarnación in 1974**, **, *** (DUSS).

Additional specimens examined:

PERU. LIMA: At Lima-Oroya railway between Surco and Matucana, 2,000–2,400 m, *Weberbauer 5217* (F, G, GH, POM, US). Matucana, 2,400 m, *Asplund 10994* (RSA, UPS); *Rauh in 1954* (RSA). Vicinity of Surco, *Ferreyra 9657* (USM). Puruchuca near Matucana, *Mathews 492* (K). Near Canta, 2,200–2,500 m, *Acleto 605* (USM). *N.N. in 1950* (USM). Without exact locality: *Martinet in 1878* (P), *Martinet 71* (P).

Oenothera featherstonei has flowers as large as those of *O. odorata* and *O. ravenii*. Its area of distribution presumably extended to lower elevations along the coast of Peru during the Pleistocene. *Oenothera nocturna*, its complex heterozygote derivative, still coexists in these areas with *O. laciniata* subsp. *pubescens*. The spread of *O. nocturna* may have played a role in limiting the range of *O. featherstonei* to its present very limited area. Plants with 8 or 10 rings of chromosomes at meiotic metaphase I may represent hybrids between *O. featherstonei* and *O. nocturna*. On the basis of its nearly black seeds and strigillose pubescence, which gives the plants a grayish hue, one might hypothesize that *O. featherstonei* may have been derived from an ancestral form similar to *O. peruana* (series *Renneria*), the least specialized of all species of subsect. *Munzia*.

34. **Oenothera nocturna** Jacq., Coll. 3: 205. 1789; Icon. Pl. Rar. 3: 3, *tab.* 455. 1791.—FIGS. 155, 190, 224.

O. albicans Lam., Encycl. Méth. 4: 552, *tab. 279, fig. 2.* 1797. TYPE: not seen. The illustration in Encycl. *tab. 279* represents the species here described.

O. prostrata Ruiz & Pavón, Fl. Peruv. Chil. 3: 79, *tab. 315.* 1802. LECTOTYPE: Peru, Dep. Lima, common in the provinces of Lima and Chancay, *J. Dombey* (P).

Onagra nocturna (Jacq.) Moench, Suppl. Meth. Pl. 287. 1802.

Onothera polymorpha H. Lév. race *longiflora* (Jacq.) H. Lév. var. *nocturna* (Jacq.) H. Lév., Monogr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 324. 1909.

Raimannia nocturna (Jacq.) Sprague & Riley, Kew Bull. 1921: 201. 1921.

Oenothera laciniata Hill var. *nocturna* (Jacq.) Munz, Amer. J. Bot. 22: 656. 1935.

O. laciniata sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 537. 1941, pro parte.

Erect annual to perhaps sometimes perennial herb, forming a weak rosette, well branched near the base, 3–6 dm tall. Plants exclusively strigillose. Cauline leaves elliptic or narrowly lanceolate to lanceolate, acute, narrowly cuneate at the base, short-petiolate, 4–6 cm long, 0.5–1.5 cm wide; bracts narrowly elliptic to lanceolate, acute, acute at the base, 1.5–3 cm long, 0.5–1 cm wide; leaves plane to slightly undulate at the margins, ± regularly sinuate. Inflorescence usually branched. Floral tube 1.5–2.5 cm long. Buds oblong in outline, 0.5–1 cm long, 3–4 mm thick; apices of the sepals 1.5–2.5 mm long, divergent. Petals very broadly obovate, 1–1.5 cm long. Anthers 4–7 mm long. Filaments 6–13 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2–3.2 cm long. Stigma lobes 3–5 mm long. Ovary 1–1.3 cm long. Capsule 1.8–2.5(–3) cm long, 2.5–3.5 mm thick. Seeds elliptic to broadly elliptic in outline, 1.3–1.8 mm long, 0.8–0.9 mm thick, dark brown to almost black. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: At high elevations, February–June; at low elevations, September–November.

Neotype: Jacq., Icon. Pl. Rar. 3: *tab. 455.* 1795. No specimen collected before 1792 seems to have persisted, but the identity of this taxon is made clear by the plate selected as the neotype, and by the following two old cultivated specimens labeled with this name: Hort. Kew, 1792 (BM). Cult. Hort. Paris, Oct. 1815, Herb. J. Gay (GH, K). It was said to be from the Cape of Good Hope, but no African material has been seen; the original seeds undoubtedly came from the vicinity of Lima or elsewhere in Peru, to which the species is endemic.

Distribution (Fig. 239): Predominantly at lower elevations in the departments of La Libertad, Lima, Huancavelica, and Ancash, Peru, but ascending into the mountains along river valleys to 3,200 m elevation.

Specimens examined from cultivated plants:

PERU. LIMA: Valley of Río Rimac, at the road and on dry slopes, between the road (km 74.9–76.1) and the railroad (km 99–100) from Lima to Oroya, near Matucana, ca. 2,200 m, *Santarius 2327**, *2328**, *2333** (DUSS, MO: *2328* also CTES, M).

Additional specimens examined:

PERU. LA LIBERTAD: In valley between Pacasmayo and railhead, 2,130 m, *Forbes in 1912* (BM). Trujillo, Barranza, 60 m, *Sagástegui 7857* (CTES, MO). ANCASH: Recuay near Marca, 2,600 m, *Gómez 38* (USM). Carancayo in valley Fortaleza near Bolgnesi, 2,600 m, *Cerrate 12188* (BM, USM). Taclán, 3,050–3,100 m, *Proaño 87* (USM). LIMA: Lima, *Savatier 1395* (K), *Martinet 40 (882)* (P, US); *Anderson in 1852* (S); *Mathews 493* (K). San Agustín, *Asplund 13824* (RSA). San Boskobo, 120–240 m, *Saunders 163* (BM). Lomas de Lurín, 400–500 m, *Ferreyra 9536* (BM, USM). Lomas de Atocongo, 300–400 m, *Ferreyra 0172, 2062, 12478* (USM); *Aguilar in 1948* (USM); *Pennell 14777* (F); *Vargas et al. 9296* (GH, K, UC). Chancay, *Dombey 727* (G, L, P). *Vargas 4710* (MO). Ruins of Cajamarquilla near Chancay, 300–400 m, *Ferreyra 2838* (USM). Supe, near Chancay, 100 m, *Goodspeed et al. 17361* (UC). Lomas de Lachay, between Chancay and Huacho, 400–500 m, *Ferreyra 8770, 11503* (USM); *Infantes 2128* (LIL); *Cerrate 856* (BM, USM). Madalena near Lima, *Née* (F). San Isidro, *Raimondi 6115* (USM). Miraflores, *Maisch 13727* (USM). Amancae, *Jaffuel 3934* (GH). River Rimac, 1,220 m, *Safford in 1887* (NY); *Ball 1882* (GH pro parte, K, NY). Chosica, *Martinet 40* (P, RSA). Huaquicha near Surco, 2,600–2,700 m, *Ferreyra 6067* (US, USM). Surco, 2,000 m, *Asplund 11056* (RSA). Santa Eulalia valley near Huarochiri, *Mc. Hanrish 13*, 14 (K). Matucana, *Raimondi in 1877* (USM). Mountains E of Tupe, Atsmito, 3,100 m, *Cerrate 1059* (BM). Canta, 3,000–3,200 m, *Pennell 14603* (F, GH). Cajatambo, 2,740 m, *Sandeman 5322* (K). HUANCAVELICA: Córdoba near Castrovirreina, 3,050–3,300 m, *Metcalf 30288* (G, GH, MO, UC, US).

Cultivated specimens:

Erlangen, Germany, 1795, Herb. *Schreber 159* (M; as *O. capensis*). Erlangen, *in 1800* (M). Botanical Garden of Göttingen, Germany, *in 1803* (LE).

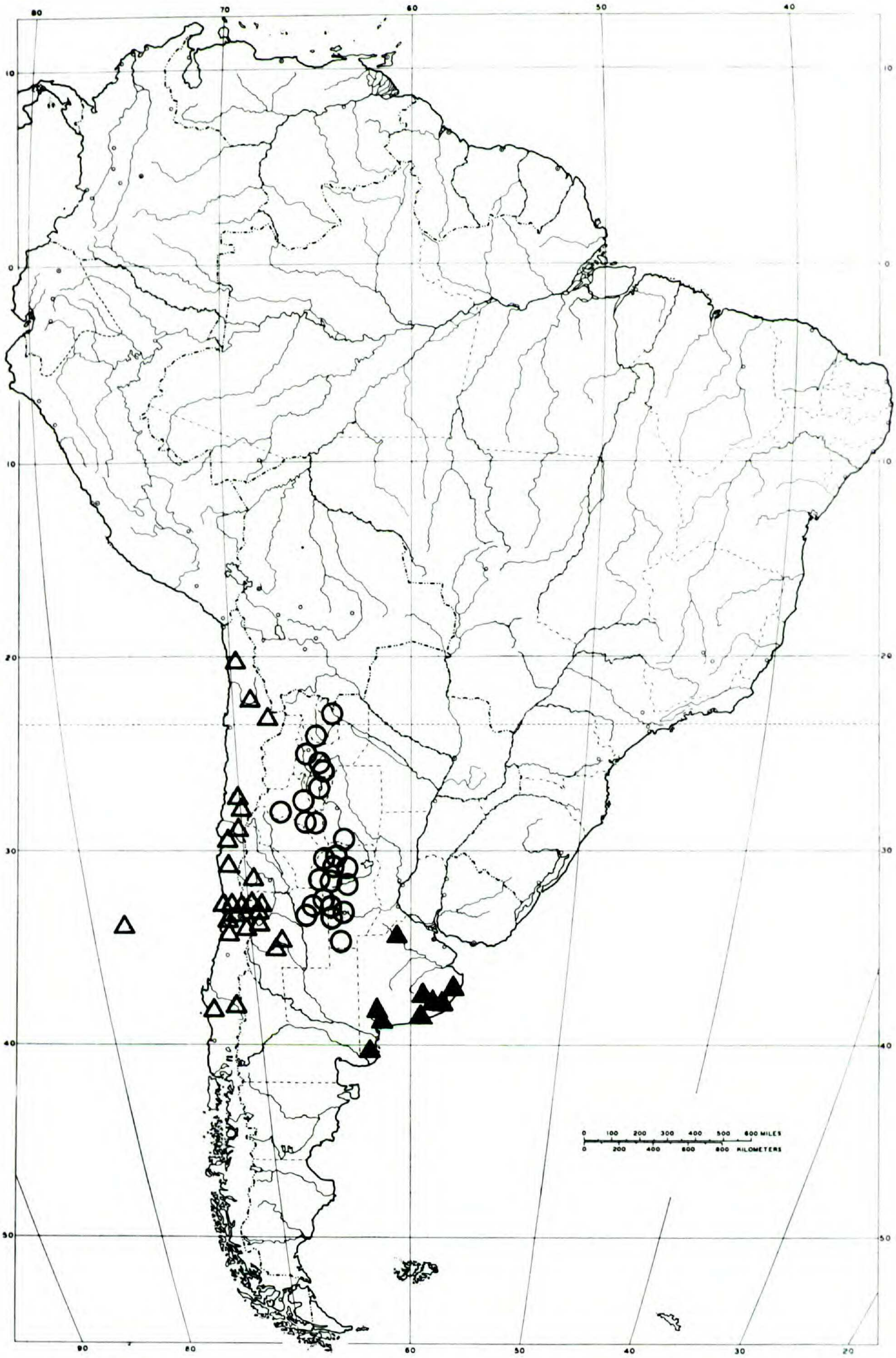


FIGURE 237. Ranges of *Oenothera picensis* subsp. *picensis* (hollow triangles), *O. picensis* subsp. *cordobensis* (circles), and *O. picensis* subsp. *bonariensis* (filled triangles).

The complex heterozygote *O. nocturna* may be separated from the bivalent-forming *O. featherstonei* by its smaller flowers, autogamous breeding system, and usually sinuate leaves. The overwhelming morphological similarity between these species leaves no doubt that *O. featherstonei* contributed one of the chromosomal complexes to *O. nocturna.* The pitting of the seeds in *O. nocturna* (Fig. 190) is very similar to that in *O. laciniata* subsp. *pubescens* (subsect. *Raimannia*). It seems possible that *O. laciniata* subsp. *pubescens* has contributed a genome to *O. nocturna*, and perhaps also to *O. arequipensis* (the other parent being *O. verrucosa*), but these hypotheses have not yet been tested experimentally. Neither *O. nocturna* nor *O. arequipensis* has the nodding buds characteristic of *O. laciniata* subsp. *pubescens.*

Series III. CLELANDIA

Oenothera sect. **Oenothera** subsect. **Munzia** series **Clelandia** Dietrich, ser. nov.

Raimannia sensu Sprague & Riley, Bull. Misc. Infor. 1921: 200. 1921, pro parte.
Oenothera § *Raimannia* sensu Munz & Johnston, Contr. Gray Herb. 75: 16. 1925, pro parte.
Oenothera subgen. *Raimannia* sensu Munz, Physis 11: 279. 1933, pro parte; Amer. J. Bot. 22: 645. 1935, pro parte.

Herbae annuae vel biennes (*O. punae* perennis est), erectae vel prostratae, rosulatae vel erosulatae. Capsula sursum gradatim angustata, specieribus paucis cylindricis, ± erecta, manifeste bractea subtenta connata; valvulae capsulae post dehiscentiam extro curvatae.

Annual or biennial herbs (only *Oenothera punae* perennial), erect or prostrate, forming a rosette or the stem elongating soon after germination, unbranched or with oblique or arching side branches arising from the rosette; plants 2–15(–20) dm tall, or with prostrate branches 5–25 cm long. Stems usually thicker than those of series *Allochroa*, (3–)5–15 mm thick. Plants (1) densely to sparsely strigillose and densely to sparsely long- and short-villous; (2) densely to sparsely strigillose, densely to sparsely long- and short-villous, and moderately to sparsely glandular-pubescent; or (3) densely to sparsely long- and short-villous and densely to sparsely glandular-pubescent. Rosette leaves linear to narrowly oblong, very narrowly elliptic to elliptic or narrowly oblanceolate, gradually narrowed to the petiole or subsessile and narrowly cuneate at the base, 2–25 cm long, 0.1–2.5 cm wide; cauline leaves linear to narrowly oblong, very narrowly elliptic to elliptic or narrowly lanceolate to lanceolate, acute, narrowly cuneate to truncate at the base, sessile or short-petiolate, 1.5–20 cm long, 0.1–2 cm wide; bracts linear, very narrowly elliptic to narrowly elliptic or narrowly lanceolate to narrowly ovate, acute, acute to subcordate at the base, 1.5–6 cm long, 0.1–1.5 cm wide, often with red margins; leaves plane or evidently undulate at the margins, usually irregularly serrate with blunt or sharp teeth. Inflorescence simple or branched; flowers erect or somewhat oblique with respect to the stem. Floral tube 0.5–10 cm long. Buds narrowly oblong to oblong, elliptic to broadly elliptic, or narrowly lanceolate to lanceolate in outline, green to yellowish, often flushed with red, often with red stripes at the junction of the sepals with the floral tube, 0.3–2.5 cm long, 2–6 mm thick. Sepals rarely flecked with dark red; apices of the sepals 0.5–3 mm long, erect

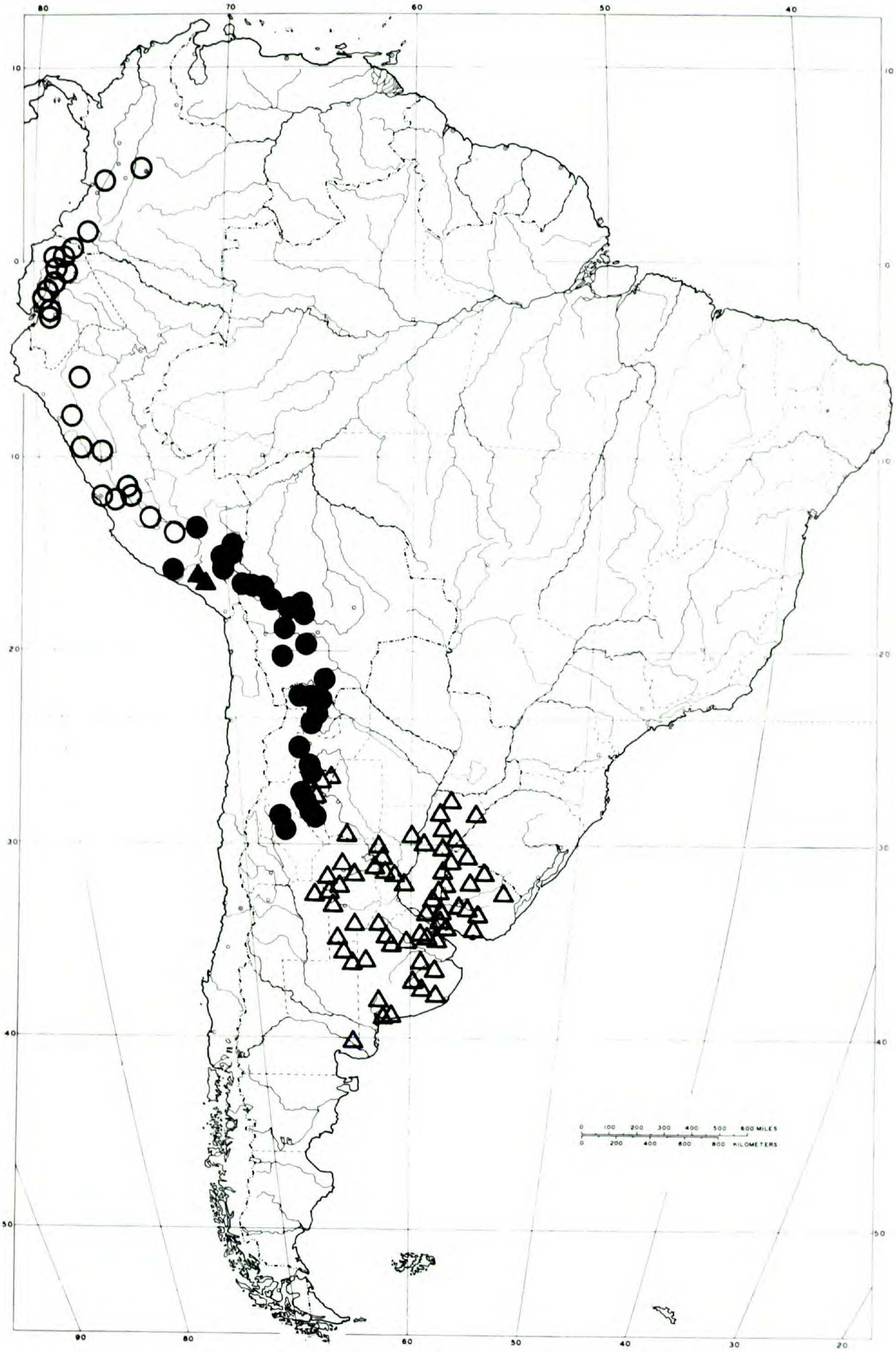


FIGURE 238. Ranges of *Oenothera parodiana* subsp. *parodiana* (hollow triangles), *O. punae* (dots), *O. verrucosa* (filled triangles), and *O. laciniata* subsp. *pubescens* (circles).

or divergent. Petals obovate to very broadly obovate, 0.4–3 cm long, yellow, rarely with an indistinct red spot at the base of each one. Style short, the anthers shedding pollen directly on the stigma at anthesis. Ovary 0.5–2 cm long. Capsule 1.2–4 cm long, 2.5–5 mm thick, in most species gradually narrower upward from a broad base, in a few broadly cylindrical, ± erect, evidently fused with the subtending bract; valves curving outward as in series *Allochroa* when the capsule sheds its seeds. Seeds elliptic to rotund in outline, 0.8–2 mm long, 0.5–0.9 mm thick, light to dark brown, sometimes flecked with dark red-brown spots. Self-pollinating complex heterozygotes. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I; plants with smaller rings very rare).

Type species: *Oenothera elongata* Rusby.

Distribution (Fig. 7): Most species of this series occur at low elevations. Only the species that occur in Bolivia and *O. punae* are characteristic of the high mountains.

This series is dedicated to the late Ralph E. Cleland (1892–1971), student of *Oenothera.* All of the species assigned to it combine one genome derived from series *Renneria* with another derived from series *Allochroa.* See also the remarks on pp. 427 and 434 concerning the relationships of this group.

Many of the species included here are relatively difficult to recognize as members of series *Clelandia* in a pressed condition. The capsules are mostly not cylindrical, however, and they do taper toward the apex. Whereas the capsules of series *Allochroa* always stand out obliquely from the stem, those of series *Clelandia* are more nearly erect, like those of series *Renneria.* In complex heterozygotes that involve *O. affinis*, however—at least in *O. elongata* and *O. pseudoelongata*—the capsules are cylindrical, which might be related to the fact that the capsules in *O. affinis* are somewhat swollen in their upper third. The inflorescence of series *Clelandia* is, as a rule, thicker and more heavyset than that in series *Allochroa.*

35. **Oenothera magellanica** Philippi, Anales Univ. Chile 84: 633. 1893.—Figs. 83, 156.

O. hirsuta Meigen, Bot. Jahrb. Syst. 17: 260, 291. 1893; non (Spach) Steud., Nom. Bot., ed. 2. 2: 206. 1841. LECTOTYPE: Chile, Yerba Loca, 2,000 m, 7 Aug. 1892, *F. Meigen* 539 (SGO, GH photograph).

O. magellanica Philippi var. *chubutensis* Macloskie, Rep. Princeton Univ. Exped. Patagonia 8 (5, 3): 613. 1905. TYPE: not located.

Oenothera stricta sensu Macloskie, Rep. Princeton Univ. Exped. Patagonia 8(5, 3): 614. 1905; sensu Munz, Physis 11: 284. 1933, pro parte; Amer. J. Bot. 22: 661. 1935, pro parte; sensu Bøcher, Dansk Bot. Ark. 22: 90. 1968.

Onothera polymorpha H. Lév. race *odorata* (Jacq.) H. Lév. var. *magellanica* (Philippi) H. Lév., Monogr. Onoth. 363. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.

Oenothera mollissima sensu Munz, Physis 11: 282. 1933, pro parte; sensu Bøcher, Dansk. Bot. Ark. 22: 90. 1968.

Oenothera odorata sensu Munz, Physis 11: 284. 1933, pro parte; Amer. J. Bot. 22: 660. 1935, pro parte; Revista Univ. (Santiago) 22: 264. 1937, pro parte.

Erect annual or biennial herb, forming a rosette, unbranched or with a branched main stem and arching or obliquely ascending side branches arising

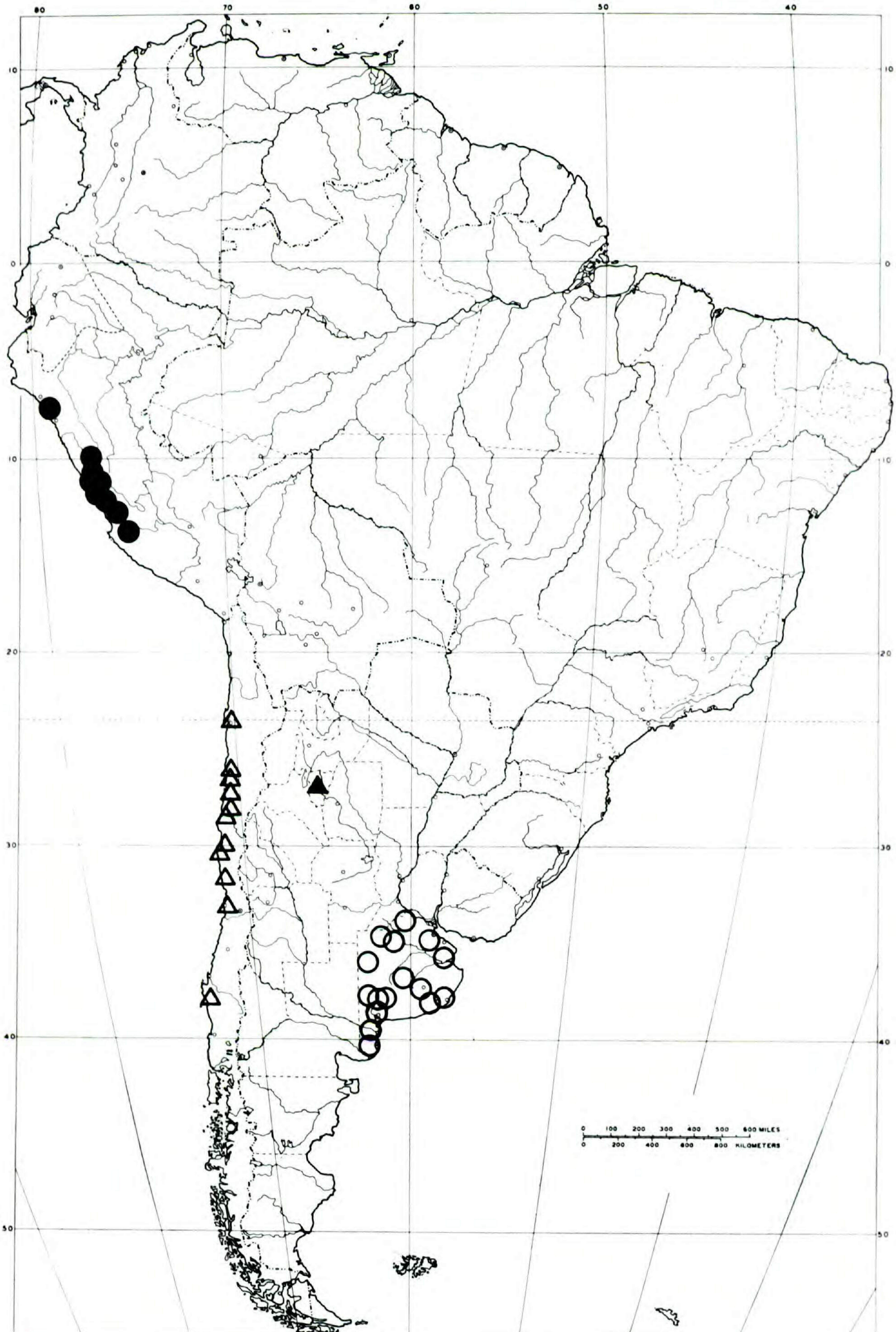


FIGURE 239. Ranges of *Oenothera parodiana* subsp. *strigulosa* (circles), *O. acuticarpa* (filled triangle), *O. coquimbensis* (hollow triangles), and *O. nocturna* (dots).

from the rosette, 2–12 cm tall. Plants densely to very sparsely strigillose, moderately to sparsely long- and short-villous, rarely sparsely glandular-pubescent. Rosette leaves linear to narrowly oblanceolate, acute, gradually narrowed to the petiole, 10–25 cm long, 0.9–1.5 cm wide; cauline leaves very narrowly elliptic to narrowly lanceolate or narrowly oblanceolate, acute, narrowly cuneate to attenuate at the base, sessile, 5–20 cm long, 0.5–1.2 cm wide; bracts narrowly lanceolate to lanceolate, acute, rounded to truncate at the base, sessile, longer than the capsules they subtend, 4–6 cm long, 0.5–1 cm wide; leaves plane or markedly undulate at the margins, regularly or irregularly serrate, the teeth blunt or sharp. Inflorescence simple or branched. Floral tube 1.3–2.5(–3) cm long. Buds oblong to lanceolate in outline, green to yellowish green, often flushed with red, 1–2 cm long, 4–5 mm thick; apices of the sepals 1–2 mm long, erect or divergent. Petals very broadlly obovate, 1.5–2.5 cm long. Anthers 6–8 mm long. Filaments 9–12 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.5–4.5 cm long. Stigma lobes 3–5 mm long. Ovary 1.5–2 cm long. Capsule 2.5–4 cm long, 3–5 mm thick. Seeds elliptic in outline, 1.4–2 mm long, 0.6–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14*, ring of 12 and 1 bivalent**, ring of 8 and ring of 6*** or ring of 10 and 2 bivalents**** at meiotic metaphase I). Flowering time: Northern area, November–April; southern area, November–March.

Lectotype: Argentina, Prov. Santa Cruz, Río near Lago Argentino (Lago Santa Cruz), 15 Feb. 1879, _E. Ibar_ (_2187_) (SGO-041392, GH photograph).

Distribution (Fig. 232): Most frequent along the western foothills of the Andes in the provinces of San Juan, Mendoza, Neuquén, Río Negro, Chubut, and Santa Cruz in Argentina, but with isolated stations in the provinces of Aconcagua, Santiago, Aisén, and Magellanes in Chile, and very widely scattered localities in the provinces of Córdoba, San Luis, and Buenos Aires (Bahía Blanca), Argentina.

Specimens examined from cultivated plants:

ARGENTINA. SAN JUAN: Dep. Iglesias, Tocota, 2,480 m, _Ruizthal in 1962*_ (DUSS, MO). MENDOZA: Stony slopes at Ruta 7, 1 km of Punta de Vacas, 2,500 m, _Santarius 1459*_, _1461_, _1464_, _1467*_, _1475_ (DUSS; _1459_, _1467_ also M; _1467_ also MO). Dry rivulet bed near Ruta 7, 4.5 km E of Punta de Vacas, 2,450 m, _Santarius 1476*_, _1480_, _1483_, _1485_, _1489*_, _1490_, _1492*_, _1496_ (DUSS; _1480_, _1489_ also CTES, M, MO). Stony slope along Ruta 7, 1 km W of Polvaredas, 2,450 m, _Santarius 1504*_, _1506_, _1513*_, _1518_ (DUSS; _1504_ also MO). Arroyo Polvaredas E of Polvaredas, 2,400 m, _Santarius 1523*_, _1525_, _1526*_, _1528*_, _1532_, _1534_, _1536_, _1540_, _1541*_, _1544_, _1548*_ (DUSS; _1526_, _1528_, _1541_, _1544_, _1548_ also CTES, M, MO). Waste and stony places ca. 2 km N of Tupungato 1,250 m, _Santarius 1562*_ (DUSS). Rocks and stony slopes of the Precordillera near Villavicencio, 12 km above Villavicencio on Ruta 7, 2,600 m, _Santarius 1577*_, _1578_, _1579*_, _1580_ (DUSS; _1579_ also CTES, M, MO). 10.5 km above Villavicencio, 2,500 m, _Santarius 1581*_, _1582_, _1584*_, _1588*_, _1589*_, _1591*_, _1592_, _1593*_, _1595_ (DUSS; _1581_, _1584_, _1588_, _1591_, _1592_, _1593_, also CTES, M, MO). 9.5 km above Villavicencio at km 1160, 2,350 m, _Santarius 1597*_, _1598_, _1599*_, _1602*_, _1603*_, _1607_, _1608_ (DUSS; _1598_, _1599_, _1602_ also CTES, M; _1598_, _1599_, _1602_, _1607_ also MO). 9 km above Villavicencio, 2,300 m, _Santarius 1610*_, _1616_, _1621*_, _1622*_, _1625*_ (DUSS; _1621_, _1622_, _1625_ also CTES, M, MO). 5 km above Villavicencio (Los Surtidores), 2,050 m, _Santarius 1638****_, _1639_, _1641_, _1642_, _1643*_, _1646*_, _1649_ (DUSS; _1646_ also M, MO). Villavicencio, 1,700 m, _Santarius 1652*_, _1653_, _1654_ (DUSS; _1653_ also CTES, M, MO). Uspallata, _Hecht 1964–79*_ (DUSS). NEUQUÉN: Stony places at Río Limay, 6 km E of Piedra del Águila, _Santarius 607*_, _609*_ (DUSS, M, MO; _607_ also CTES). Stony places near the ferry across Río Limay at Ruta 237, ca. 75

km SSW of Piedra del Águila, *Santarius 645** (CTES, DUSS, M, MO, SP). RÍO NEGRO: San Carlos de Bariloche, *Stubbe in 1961** (CTES, DUSS, M, MO). Sandy and stony waste places at the shore of the Lago Nahuel Huapí, near railroad station of Bariloche, 780 m, *Santarius 646**, *647*, *649**, *652*, *655*, *656**, *657*, *659*, *661*, *663**, *668**, *674*, *676*, *677*, *692*, *694*, *700*, *706**, *709*, *734*, *736*, *744*, *751* (DUSS; *649*, *657*, *668*, *677*, *706* also CTES; *646*, *649*, *657*, *668*, *677*, *706* also M; *646*, *649*, *657*, *668*, *676*, *677*, *706* also MO). N slope of Cerro Otto, ca. 3 km W of Bariloche, along road to the top on volcanic ashes, 850 m, *Santarius 784**, *786*, *789**, *796*, *797* (DUSS; *784*, *789* also CTES, M, MO). El Bolsón, 325 m, *Santarius 838*, *840**, *842*, *847*, *851* (DUSS; *840* also CTES, MO). NW slope at km 17.5 of the road from Bariloche to Villa Catedral, 1.5 km N of Villa Catedral, 900 m, *Santarius 853** (DUSS, MO). CHUBUT: Meadows about 11.5 km SSW of El Bolsón on the road to Lago Puelo, 300 m, *Santarius 821** (DUSS). Airport of Esquel, 675 m, *Santarius 903**, *904*, *905*, *907**, *910*, *912* (DUSS; *903*, *907* also CTES, M, MO); ibid., *Santarius 1393**, *1394*, *1398**, *1404* (DUSS; *1393* also M, MO). SANTA CRUZ: Dry rivulet bed 2 km N of bridge on Ruta 3 across Río Gallegos, *Santarius 997** (DUSS). Dep. Lago Argentino, Parque Nacional Los Glaciares, N slopes near Guardabosque about 48 km WSW of Calafate, 200 m, *Santarius 1067**, *1070*, *1074–1076*, *1081**, *1086**, *1088*, *1089**, *1090–1092* (DUSS; *1086* also M; *1081*, *1086* also MO). Above the campgrounds ca. 51 km WSW of Calafate, 250 m, *Santarius 1095**, *1102*, *1104*, *1108*, *1111*, *1116*, *1121*, *1122*, *1126* (DUSS; *1104* also MO). Road ca. 1 km S of Punta Bandera near Lago Argentino, 200 m, *Santarius 1128**, *1130* (DUSS). Road to Punta Bandera near fork to Ventisquero Moreno, 250 m, *Santarius 1133**, *1135*, *1138*, *1147**, *1148*, *1150*, *1159* (DUSS; *1133* also MO). Stony and sandy places near Perito Moreno, 380 m, *Santarius 1254**, *1255*, *1260*, *1268**, *1269*, *1270**, ** (DUSS; *1254* also MO). 4 km W of Estancia Las Chilcas, ca. 46 km W of Perito Moreno, 250 m, *Santarius 1338**, *1339*, *1344*, *1345* (DUSS). Río Los Antiguos W of Los Antiguos, 220 m, *Santarius 1303**, *1304–1306*, *1309*, *1311*, *1315**, *1316**, *1317*, *1320**, *1321*, *1322*, *1323** (DUSS; *1306* also CTES; *1303*, *1306*, *1316* also M; *1303*, *1306*, *1320*, *1322* also MO).

CHILE. AISÉN: Puerto Ibáñez at Lago Buenos Aires, on stony places on the sea shore and slopes up to 300 m above lake, *Nodt in 1961* (DUSS). Waste places, shore of Lago Buenos Aires in Chile Chico, 210 m, *Santarius 1286**, *1287*, *1290*, *1292*, *1295*****, *1298**** (DUSS; *1286* also M, MO). MAGELLANES: Road 0–4 km E of Puente Lago Amarga, W of Lago Sarmiento and S of Lago Nordenskjold, 150 m, *Santarius 998**, *1001**, *1004**, *1007*, *1011*, *1014*, *1023**, *1024*, *1025**, *1028*, *1036*, *1037*, *1041* (DUSS; *998*, *1001*, *1023*, *1025* also M; *998*, *1001*, *1004* also MO).

Representative specimens examined:

ARGENTINA. SAN JUAN: Bajada de Cuesta Vieja, *Hossens 2578* (CORD). Valley of Río de Los Chupadores, *Hossens 2537* (CORD). Leoncito, *Schegaray in 1876* (CORD). Dep. Sarmiento, El Federal, *Cuezzo 1705* (LIL, RSA). Arroyo los Dos Puentes near Iglesias, *Spegazzini 231* (BAB). Road from Portezuelo to Agua Negra, 3,100 m, *Fabris et al. 8383* (LP, SI). MENDOZA: Villavicencio, 2,900 m, *Boelcke 9955* (BAA, BAB); *Bartlett 19424* (GH, MICH, UC, US); *O'Donell 1019* (LIL); *Roig 5305* (CORD); *Sparre 1498* (S); *Nicora 4334* (SI). Puente del Inca, *Kurtz 3504* (CORD). Punta de Vacas, *Haumann in 1918* (BA). Las Heras, Quebrada del Toro, *Lourteig 816* (LIL, NY). Dep. Luján, Est. El Salto, 2,950 m, *Ruiz Leal 6183* (Leal). Dep. Malalhue, Los Molles, 1,850–1,950 m, *Ruiz Leal 20887* (Leal). Tupungato, *Ruiz Leal 2784a* (Leal, POM). San Rafael, Minacar at Río Grande, 2,500 m, *Lourteig 734* (LIL). Cerro Diamante, *Gillies* (K). Cerro Nevado, *Ruiz Leal 2506* (Leal, POM). Arroyo Mangas in valley of Río Atuel, 1,900 m, *Wilczek 411* (G, US, Z). Banks of Río Atuel near El Sosneado, *Burkart et al. in 1942* (SI). Refugio Gral, Alvarado near San Carlos, *Cuezzo & Barkley 20Mz475* (LIL). Campo de los Andes near Tunuyan, 1,800 m, *Araque 1126* (LIL). Gral. Gutierrez near Maipú, *Ruiz Leal 25-2108* (POM). NEUQUÉN: Traful, *Cabrera & Job 397* (LP, NY). Est. La Primavera, *Castellanos in 1938* (RSA). Between Pulmari and China Muerta, *Maldonado 669* (F). Between Ñorquin and Codihue, *Kurtz 6287* (CORD). Las Lajas, *Spegazzini 100* (BAB). Lago Nonthué, between Puerto de Gendarmeria and Arroyo near Hua Hum, *Valla 3286* (BAA). Paso Flores at Río Limay, *in 1938* (LIL-80006). Aluminé, *Giacobbi 12935* (BAA, POM). Santa María at Lago Nahuel Huapí, *Ljunguer in 1934* (NY). RÍO NEGRO: San Carlos de Bariloche, *Lesse 19* (P); *Buchtien 1356* (BREM pro parte, GH pro parte); *Meyer 7543* (LIL, NY). Cerro Otto, *De Barba 945* (LIL, RSA); *Boelcke 1702* (CTES). Arroyo Ñireco near Bariloche, *Meyer 8060* (LIL). Laguna Cari Lauquén, *Kurtz 6110* (CORD). El Bolsón, *De Barba 422* (F, LIL). Perito Moreno, *Novatti 10* (LP). Gral. Conesa, *Meyer 7119* (LIL). Choele Choel, 152 m, *O'Donell 795* (LIL). CHUBUT:

Between El Bolsón and Colonia 16 de Febrero, *Illin 237* (BR, CORD, HBG, SI). Tehuelches, between Gob. Costa and José de San Martín, *Moreau 3619* (BAB). Valley of Río Chubut, *Koslowsky 31-1643* (POM). Est. Leleque near Cushamen, *Meyer 7776* (GH, LIL). Río Percey, *Kühnemann 648* (RSA). Cordillera, Río Corcovado, *Illin 40* (UC). Dep. Escalante, Est. Los Manantiales near Cañadón Pilar, 380 m, *Eyerdam et al. 23800* (G, GH, MO, S, UC). Lago Epuyén, *Soriano 1365* (BAA). Esquel, *Garcés 286* (SI). SANTA CRUZ: Río Gallegos, *Tauber 89* (BR). Cañadón León, *Cittadini 20* (BAB). Puerto Deseado, *Correa 3300* (BAA, BAB, MO). Güer Aike, *O'Donell 4070* (LIL, RSA). Lago Viedma, 300 m, *Donat in 1932* (POM). Río Oro, *Donat 335* (SI). Lago Posadas, 200 m, *Donat 256* (BM, F, G, GH, HBG, K, LIL, MO, NY, S, SI, UC, Z). Junction of Río Blanco and Río Electrico, 720 m, *Luti 3726* (CORD). Calafate at Lago Argentino, *Hicken & Haumann 607* (SI). Between Lago Argentino and Lago Viedma, *Eyerdam et al. 24347* (GH, K, UC). Lago Buenos Aires, *Skottsberg 657* (S). CÓRDOBA: El Durazno near Punilla, *Meyer & Sleumer 15669* (LIL). Pampa de Achala, *Meyer & Sleumer 15533* (LIL). Copina, *Burkart 7326* (LIL). Valle de los Reartes, *Castellanos in 1920* (LIL). Quebrada del Tigre near San Javier, *Bridarolli 1582* (LP). SAN LUIS: Sierra de Comechingones, El Rincón, *Hunziker 11828* (CORD). El Morro, 1,100 m, *Hunziker 12596* (CORD); *Pastore in 1913* (SI-4671). El Rincón, *Conrad & Dietrich 144, 146, 148, 150, 153* (DUSS). BUENOS AIRES: Bahía Blanca, *Claraz 218* (G).

CHILE. ACONCAGUA: Juncal, 2,200 m, *Buchtien in 1903* (BM, BREM, GH, L, LY, M, S, SI, US, W). Road to Argentina, at Río Blanco, *Nicora 4397* (SI). SANTIAGO: Río Yeso near Romeral, *Biese in 1944* (LIL). San Gabriel, 1,500 m, *Montes 527* (K, MO). AISÉN: Valle Coihaique, *Rentzell 6129* pro parte (GH). Est. El Paine, *Paschke 12246* (CONC). Salto Grande del Paine, *Pisano 2342* (CONC). Mina Silva at Lago Buenos Aires, *Heim in 1939* (Z). Chile Chico at L.B.A., *Pfister 18480* (CONC). Valle Ibáñez, *Belem 22799* (CONC). Aisén, *Dusén in 1897* (CORD), *486* (S). MAGELLANES: Lago Sarmiento near Puerto Natales, *Rüe in 1958* (P). Ultima Esperanza, *Magens in 1954* (CONC). Laguna Mantecón near Punta Arenas, *Cekalovic in 1950* (CONC). Isla Grande I, *Gusinde 189* (W).

Specimen from plants cultivated in garden:
Botanical Garden Kew, England, *in 1873* (K; as *O. biennis* var. *undulata*).

This species derives its genomes from *O. santarii* and *O. odorata*. Experimental hybridization with these species has established the origin of *O. magellanica* beyond any doubt. Together with *O. odorata*, *O. magellanica* is the most frequent species of this section in southern South America, and the two often grow together. It can be distinguished from *O. odorata* by an array of the characteristics it has obtained from *O. santarii*: upright habit, heavier stems, smaller flowers. From *O. santarii* it can easily be distinguished by its longer fruits.

On the basis of a general similarity in habit, *O. magellanica* has often been confused with *O. stricta*, but of course that complex heterozygote has derived both of its genomes within series *Allochroa*. The short bracts of *O. stricta*, ultimately derived from *O. ravenii*, immediately separate it from *O. magellanica*.

The pattern of variation in *O. magellanica* suggests that backcrossing with *O. santarii* and *O. odorata*, with the consequent introduction of genetic material into *O. magellanica*, has been fairly frequent. Within *O. magellanica*, however, plants with anything except a complete ring of 14 chromosomes are very rare, suggesting a very high level of selection for the restoration of complex heterozygosity following hybridization. Where the range of *O. magellanica* overlaps that of *O. santarii*, the variation pattern of the former converges on that of the latter, and it begins to resemble series *Renneria* in general. The farther south one goes, however, the stronger the influence of *O. odorata* on the populations of *O. magellanica*. This influence is expressed strongly in the capsules, which become longer and more similar to those of *O. odorata* southward. The process does not go so far, however, that the boundary between the two is blurred; *O. magella-*

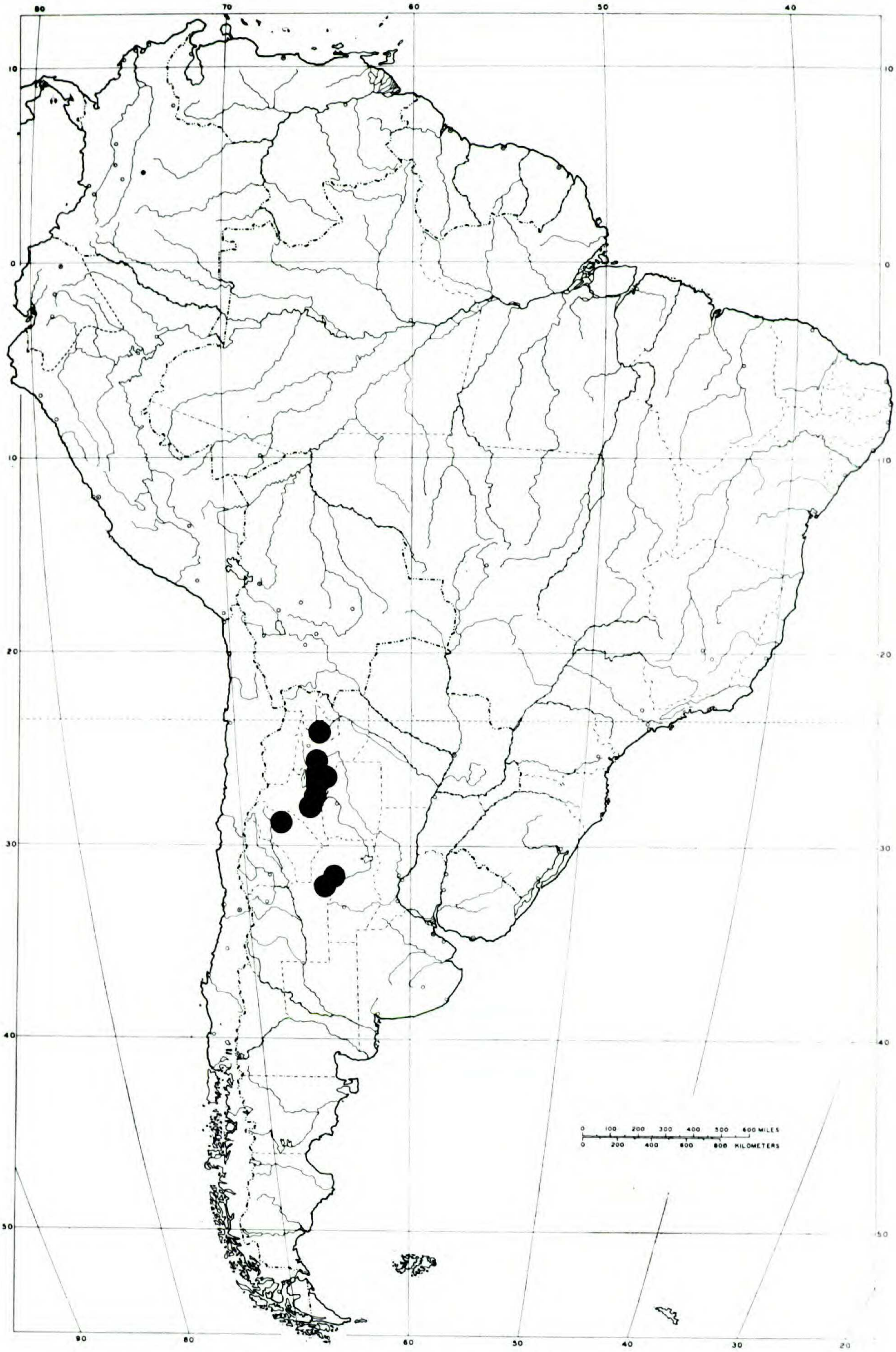


FIGURE 240. Range of *Oenothera siambonensis* (dots).

nica can always be separated easily from *O. odorata* because of its more compact inflorescence and sturdier habit. Some herbarium specimens are difficult to determine if they include insufficient or immature material; but in living plants, especially under uniform conditions of cultivation, there is never any doubt.

36. **Oenothera villaricae** Dietrich, sp. nov.—FIGS. 4, 88, 157, 205.

O. berteriana "Erlangen" Haustein, Z. Indukt. Abstammungs- Vererbungsl. 84: 418. 1952; Cleland, Jap. J. Genet. 43: 332. 1968.

Herba annua vel biennis, erecta, rosulata, simplex vel caulis principalis ramosus et ramis arcuate vel oblique e rosula ascendentibus, 5–10(–15) dm alta. Plantae densissime vel sparse strigulosae et moderate vel sparse villosae. Folia rosulae anguste elliptica vel oblanceolata, acuta, lamina in petiolum brevem gradatim decrescens vel subsessili, 10–20 cm longa, 1–2 cm lata; folia caulina anguste elliptica vel anguste lanceolata, acuta, basi acuta vel truncata, sessilia, 8–15 cm longa, 1–2 cm lata; bractea lanceolata vel anguste ovata, acuta, basi truncata, sessilia, praecipue superiora rubro-marginata apiceque incurvata, quam capsula subtena breviora vel ad eas subaequalia, raro longiora, 2–4(–6) cm longa, 0.8–1.5 cm lata; folia plerumque marginibus exigue undulatas, irregulariter obtuseque serrata. Inflorescentia plerumque simplex. Tubus floralis 2–3 cm longus. Gemmae ambito oblongae vel lanceolatae, virides vel flavovirentes, saepe rubrae, plerumque junctura sepalorum tubo florali anguste rubro-fasciatae; apices sepalorum 2–3 mm longi, erecti vel divergentes. Petala latissime obovata, interdum basi pallide rubro-maculata, 1.5–2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.3–2 cm longum. Capsula 2–3 cm longa, 3–4 mm crassa. Semina ambito late elliptica, 1.1–1.5 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual or biennial herb, forming a rosette, unbranched or with a branched main stem and arcuate or obliquely ascending side branches from the rosette, 5–10(–15) dm tall. Plants very thickly to sparsely strigillose and moderately to sparsely villous. Rosette leaves narrowly elliptic to oblanceolate, acute, gradually narrowed to the short petiole or subsessile, 10–20 cm long, 1–2 cm wide; cauline leaves narrowly elliptic to narrowly lanceolate, acute, acute to truncate at the base, sessile, 8–15 cm long, 1–2 cm wide; bracts lanceolate to narrowly ovate, acute, truncate at the base, sessile, especially the upper ones with red margins and an incurved tip, shorter than the capsules they subtend or subequal to them, rarely longer, 2–4(–6) cm long, 0.8–1.5 cm wide; leaves mostly weakly undulate at the margins, irregularly serrate with blunt teeth. Inflorescence usually unbranched. Floral tube 2–3 cm long. Buds oblong to lanceolate in outline, 1.2–1.8 cm long, 4–6 mm wide, green or yellowish green, often flushed with red, usually red striped at the junction of the sepals with the floral tube; apices of the sepals 2–3 mm long, erect or divergent. Petals very broadly obovate, sometimes with a weak basal red spot on each one, 1.5–2 cm long. Anthers 6–7 mm long. Filaments 7–11 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 3–4.5 cm long. Stigma lobes 3–4 mm long. Ovary 1.3–2 cm long. Capsule 2–3 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.1–1.5 mm long, 0.5–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–March.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 2 Aug. 1972. Source: Chile, Prov. Cautín, Molco at Lago Villarica, end of 1960, *W. Stubbe* (MO-2155226, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 234): In the Chilean provinces of Cautín, Valdívia, Osorno, Llanquihue, and on Isla Chiloe, as well as in a few localities on the eastern slope of the Andes in the Argentine provinces of Neuquén, Río Negro, and Chubut.

Specimens examined from cultivated plants:

CHILE. CAUTÍN: Sitio Göpfert at Lago Villarica, meadow above the seashore between Antumalal and Pucón, *Göpel in 1961** (CTES, DUSS, M, MO). Laguna Verde at Río Allipén near Volcán Llaima, *Göpel in 1961** (CTES, DUSS, M, MO). Molco at Lago Villarica, *Stubbe in 1960** (DUSS, M, MO). VALDIVIA: Taco Tres at Río San Pedro near Lago Rinihue, *Stubbe in 1961** (CTES, DUSS, M, MO). Las Ánimas near Valdivia, *Göpel in 1961** (CTES, DUSS, M, MO). Isla Teja in Valdivia, *Stubbe in 1960** (CTES, DUSS, M, MO). Collico near Valdivia, *Koch in 1960** (DUSS). Along the railroad near Antilhue, *Stubbe in 1961** (CTES, DUSS, M, MO). OSORNO: Stony places at S edge of Osorno, *Stubbe in 1961** (CTES, DUSS, M, MO). Pan-Amer. Highway, 5 km S Valdivia-Osorno boundary, *Wiens in 1967** (CTES, DUSS, MO).

ARGENTINA. NEUQUÉN: Pucara in the Parque Nacional Lanín, *Schachovsky in 1965** (DUSS). CHUBUT: Meadows ca. 11.5 km SSW of El Bolsón along road to Lago Puelo, 300 m, *Santarius 823*, 824, 825*, 831*, 833* (DUSS; *823* also CTES, M; *823, 833* also MO).

CULTIVATED: *O. "berteriana"* from the Botanical Garden of Erlangen in Germany, received in 1960* (CTES, DUSS, M, MO).

Additional specimens examined:

CHILE. CAUTÍN: *Calvert in 1914* (BM). Freire, *Claude-Joseph 5899* (US). Río Zuapa, *Bullock in 1905* (G). VALDIVIA: Valdivia, *Lechler* (M); *Hollermeyer 56* (S); *Buchtien in 1903* (US), *in 1898* (US); *Gay 81* (P). Railroad to Hueyelhue, *Buchtien in 1904* (M, P). Panguipulli, *Gay in 1834* (G, SGO). OSORNO: Lago Llanquihue, *Calvert in 1912* (BM). CHILOE: Canal de Dalcahue, *Funck 126* (P). Without exact locality: *Niemeyer 91* (HBG).

ARGENTINA. NEUQUÉN: Lago Quillén, *Dawson & Schwabe 2874* (BAB). RÍO NEGRO: Bariloche, *Fabris 1124* (M). El Bolsón, *Meyer 7884* pro parte (NY); *Illin 6875* (BAB).

Specimen from plants cultivated in garden:

Botanical Garden of Valence, Italy, from seeds of the Botanical Garden at Rome under the name *O. berteriana* Spach, plant of Chile, 1923, Herb. *E. J. Neyraut 14-140* (MPU). This specimen is identical with the strain known to geneticists as *O. berteriana*. Another specimen was seen from the Botanical Garden Bremen, Germany, *Fahrenholtz in 1923* (BREM).

This newly proposed species has been known to geneticists for some time, since it is identical with the "Erlangen" strain said to be *O. berteriana*. The original provenance of this line is unknown, but presumably it came from one of the provinces of Chile named above. *Oenothera berteriana* itself is a synonym of *O. affinis*.

Like *O. magellanica*, most herbarium specimens of *O. villaricae* are identified as *O. stricta*, which of course had a different origin. The *Renneria* genome of *O. villaricae* was once more contributed by *O. santarii*, whereas its *Allochroa* genome is derived from *O. ravenii* (see also Cleland, 1968). Since, as has been pointed out several times, Chile has no native chromosomally homozygous species of the subsection (except for *O. coquimbensis*), and since the main area of *O. villaricae* seems rather clearly to be Chilean, it probably originated following hybridization between *O. magellanica* and *O. stricta*.

The F_1 hybrids between *O. santarii* and *O. villaricae* consist of two classes, one like each parent. Hybridization with *O. ravenii* is only possible if that species is used as the male parent; the plastids of chromosomally homozygous *O. ravenii* from Brazil do not function in a genetic background of *O. villaricae*.

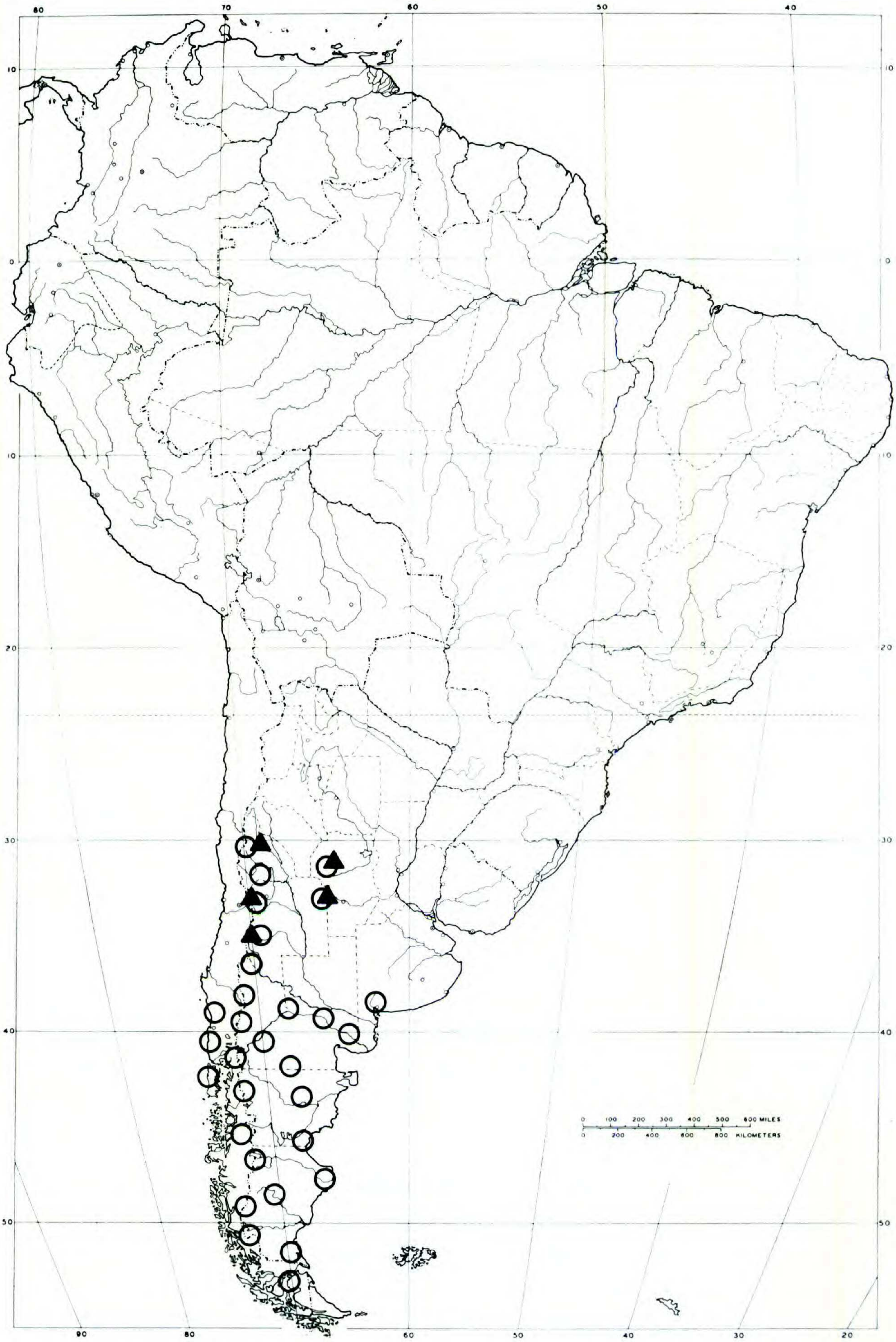


FIGURE 241. Range of homozygous *Oenothera santarii* (filled triangles) and as a chromosomal complex in *O. magellanica* and *O. villaricae* (circles).

They are colorless, and hybrids between these two species are viable only when there are sufficient green plastids derived from the *O. villaricae* parent. This is usually only the case when *O. villaricae* is the female in the hybridizations.

One of the classes of F_1 hybrids between *O. villaricae* and *O. ravenii* is identical to *O. ravenii*, but the second class does not exactly match *O. villaricae*. This is probably because the large flower size of *O. ravenii* is dominant in *O. villaricae*, and also because the *O. ravenii* complex in *O. villaricae* is derived via *O. stricta* and probably considerably altered in the course of evolution of that species.

Oenothera villaricae can be distinguished from *O. magellanica* by its shorter, red-margined bracts and shorter capsules. Both species differ from *O. stricta* in their upright, sturdy habit and more compact inflorescence.

The Argentinan plants of *O. villaricae* are somewhat different from the Chilean ones in that their bracts are usually shorter. This would seem to indicate a stronger influence of the *O. ravenii* genome. In addition, they have a somewhat more delicate habit and are consistently taller when grown under uniform cultural conditions. It does not seem desirable to separate them taxonomically, however, because they have had a common origin and are closely related. If all of the small differences within the section that are preserved by the syndrome of self-pollination and complex heterozygosity, and which have in many cases come to characterize populations, were to be recognized taxonomically, one could recognize literally hundreds of species without any gain whatsoever in taxonomic utility. Taxonomy serves its end better as a device for summarizing and grouping information about a particular group of organisms, not by splitting them into an excessive number of categories.

37. **Oenothera hechtii** Dietrich, sp. nov.—FIGS. 89–91, 158.

O. parodiana "Villa Nougues" Hecht, Indiana Univ. Publ. Sci. Ser. 16: 277. 1950; J. Hered. 61: 199. 1970.

Herba annua vel biennis, erecta, rosulata, simplex vel caulis principalis parce ramosus et ramis late arcuato e rosula ascendentibus, 5–10 dm alta. Plantae parce vel sparse strigulosae et villosae, circum inflorescentiam densiore. Folia rosulae angustissime elliptica, acuta, basi acuta, sessilia, 12–16 cm longa, 2–2.5 cm lata; folia caulina anguste oblonga vel anguste elliptica, acuta, basi acuta vel rotundata, sessilia, 6–12 cm longa, 1–2 cm lata; bractea lanceolata, acuta, basi rotundata vel truncata, sessilia, 2.5–3 cm longa, 0.8–1.2 cm lata; folia plana, irregulariter serrulata. Inflorescentia simplex. Tubus floralis 4–5.5 cm longus. Gemmae ambito lanceolatae, flavo-virentes, junctura sepalorum tubo florali rubro-fasciatae, 1.5–1.8 cm longae, 4–6 mm crassae; apices sepalorum ca. 1.5 mm longi, erecti. Petala obovata, 1.8–2.2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1–1.3 cm longum. Capsula 2.5–3 cm longa, ca. 3 mm crassa, extremi valvarum distincti, discreti, crenatique. Semina ambito late elliptica, 0.9–1.1 mm longa, 0.6–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual or biennial herb, forming a rosette, with simple or little-branched main stem and widely arching side branches arising from the rosette, 5–10 dm tall. Plant moderately to sparsely strigillose and villous, more densely so in the region of the inflorescence. Rosette leaves very narrowly elliptic, acute, attenuate at the base, sessile, 12–16 cm long, 2–2.5 cm wide; cauline leaves narrowly oblong to narrowly elliptic, acute, acute to rounded at the base, sessile, 6–12 cm long, 1–2 cm wide; bracts lanceolate, acute, rounded to truncate at the base, sessile, 2.5–3 cm long, 0.8–1.2 cm wide; leaves plane at the margins, irregularly serrulate. Inflorescence unbranched. Floral tube 4–5.5 cm long. Buds lanceolate in outline, yellowish green, red striped at the junction of the sepals with the floral tube, 1.5–1.8 cm long, 4–6 cm thick; apices of the sepals ca. 1.5 mm long, erect. Petals obovate to broadly obovate, 1.8–2.2 cm long. Anthers 5–6 mm long. Filaments 10–13 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 5–7 cm long. Stigma lobes 4–5 mm long. Ovary 1–1.3 cm long. Capsule 2.5–3 cm long, ca. 3 mm thick, with distinct, free, crenate ends to the valves. Seeds broadly elliptic in outline, 0.9–1.1 mm long, 0.6–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Argentina, Prov. Tucumán, Villa Nougés near Tucumán, *A. Hecht 1964-81* (MO-2155202, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 235): So far known only from the type locality.

Specimen examined from cultivated plants:

ARGENTINA. Prov. *Tucumán*, Villa Nougés near Tucumán, *Hecht 1964-81** (DUSS, M, MO).

This new species is dedicated to Adolph Hecht (1914–), student of *Oenothera*. Because of its superficial similarity to *O. parodiana* subsp. *brasiliensis*, it was not realized at first that *O. hechtii* belonged to series *Clelandia*. Consequently it has not yet been possible to test its parentage by experimental hybridization, although some deductions can be made on a morphological basis. Clearly, the *Allochroa* element in *O. hechtii* can have been derived only from *O. ravenii*. The rosettes of *O. hechtii* and its flowers, which have relatively long tubes and sometimes overtop the stem, are reminiscent of those of *O. longituba* of series *Renneria*.

38. **Oenothera elongata** Rusby, Mem. Torrey Bot. Club 3(3): 33. 1893.—FIGS. 159, 183.

O. serratifolia Krause, Repert. Spec. Nov. Regni Veg. 1: 168. 1905. TYPE: Bolivia, Dep. Tarija, Toldos near Bermejo, in a canyon, ca. 2,000 m, 9 Dec. 1903, *K. Fiebrig 2374* (B, destroyed in World War II, UC 292 and 689 fragments and photograph, F, GH and POM photographs; G, isotype).

Erect annual herb, not forming a rosette, unbranched or branched from the base upward, 6–15 dm tall. Plants densely to sparsely strigillose, densely to sparsely long- and short-villous, and densely to sparsely glandular-pubescent. Cauline leaves very narrowly elliptic to lanceolate, acute, attenuate to rounded at the base, 5–12 cm long, 0.5–1.5 cm wide; bracts lanceolate to narrowly ovate, acute, 2.5–5 cm long, 1–1.5 cm wide, longer than the capsules they subtend; leaves plane at the margins and remotely serrate, the teeth blunt. Inflorescence simple or branched. Floral tube 7–10 cm long. Buds narrowly oblong to lanceolate in outline, 1.5–2.5 cm long, 4–6 mm thick, often red striped at the junction

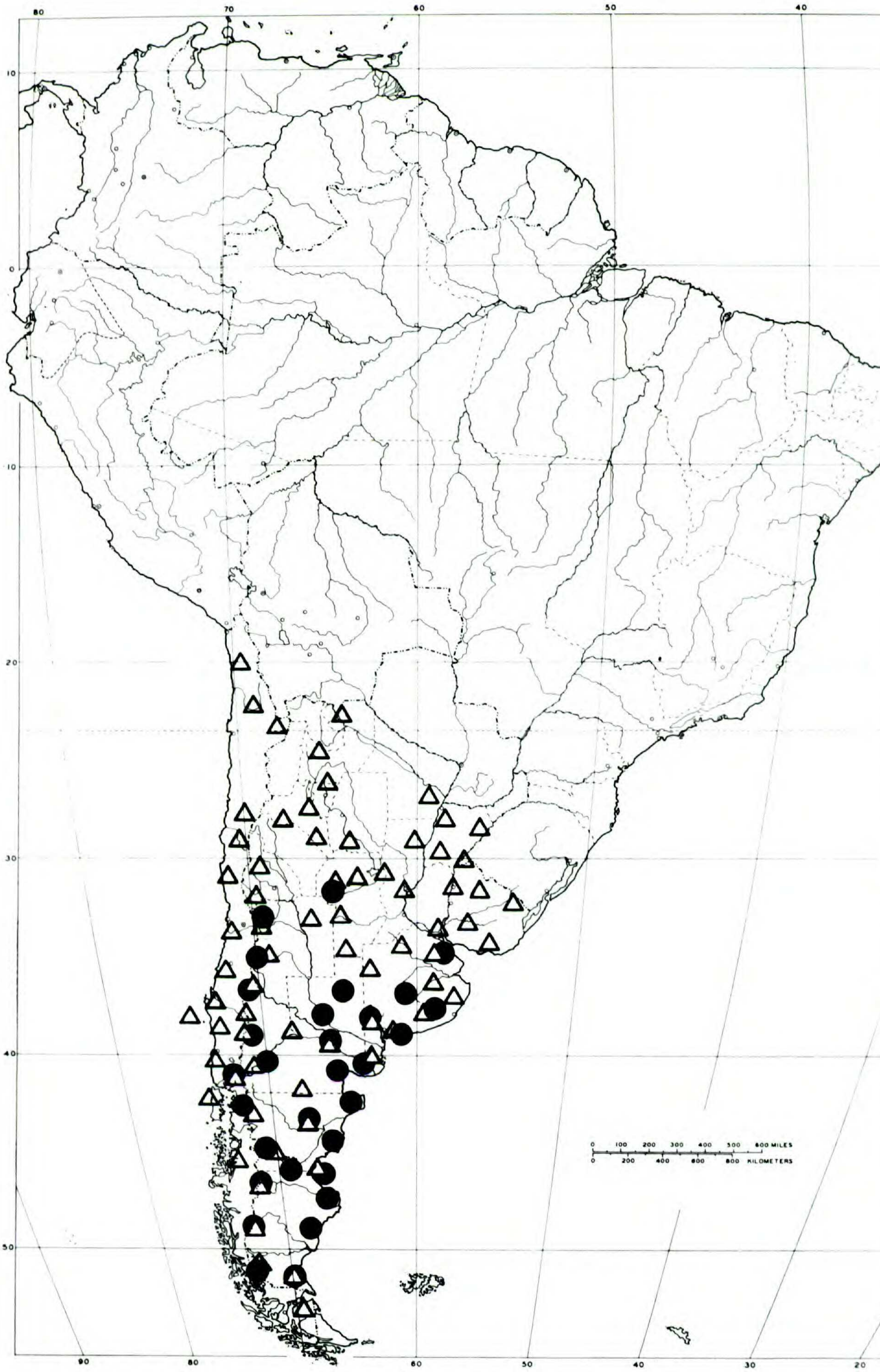


FIGURE 242. Range of homozygous *Oenothera odorata* (dots) and as a chromosomal complex in *O. grisea*, *O. magellanica*, *O. parodiana* subsp. *parodiana*, *O. picensis*, *O. rivadaviae*, and *O. stricta* (hollow triangles).

of the sepals with the floral tube and often flushed with red elsewhere; apices of the sepals 1.5–3 mm long, erect or divergent. Petals very broadly obovate, 1.5–3 cm long. Anthers 7–10 mm long. Filaments 15–24 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 8–12.5 cm long. Stigma lobes 5–7 mm long. Ovary 1.2–1.5 cm long. Capsule 2–3 cm long, 4–5 mm thick. Seeds elliptic to broadly elliptic in outline, 1.1–1.5 mm long, 0.6–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–April.

Type: Bolivia, Dep. La Paz, vicinity of La Paz, 3,280 m, 1889, *A. M. Bang 54* (NY, holotype; BM, G, GH, K, LE, MICH, MO, NY, US, W, isotypes).

Distribution (Fig. 236): Elevations of 1,200 to 3,800 m in the Bolivian Andes, in the departments of La Paz, Cochabamba, Chuquisaca, and Tarija; also an isolated station in the province of Catamarca, Argentina. See p. 439.

Specimens examined from cultivated plants:

BOLIVIA. LA PAZ: Slope on the east side of Valle de Irpavi, about 0.5–1 km N of Calacoto (SE of La Paz), above the military terrain along an irrigation ditch, 3,450 m, *Santarius 2026**, *2027*, *2028*, *2029*, *2030**, *2031–2033* (DUSS; *2026* also M; *2026*, *2028* also MO). TARIJA: Rocks and stony places along the road from Villazón to Tarija, at km 27, 2,700 m, *Santarius 1956** (DUSS); at km 26, 2,650 m, *Santarius 1957** (CTES, DUSS, M, MO); at km 25, above Tucumilla, 2,600 m, *Santarius 1958*, *1959** (DUSS; *1959* also CTES, M, MO).

ARGENTINA. CATAMARCA: La Banderita, on the road from Andalgala to Concepción (border of Prov. Tucumán), 1,800 m, *Diers in 1959** (CTES, DUSS, M, MO).

Additional specimens examined:

BOLIVIA. LA PAZ: La Paz, 3,550 m, *Buchtien 39* pro parte (C, L, LIL, M), *77* (BM, C, F, G, GH, K pro parte, LD, LIL, MO, NY, POM, SI, Z). Obrajes, 3,500 m, *Buchtien in 1907* (SI-4753); *Häberli in 1929* (Z). Prov. Larecaja, Sorata near Colani, 2,900 m, *Mandon 629* (BM, G, K, P, W). Muñecas near Charazani, 2,700 m, *Cardenas 3833* (POM). COCHABAMBA: Prov. Chaparé, 32 km NE of Cochabamba, 1,200 m, *Eyerdam 24996* (G, UC pro parte). Choro, above the Cocapata River about 100 mi NW of Cochabamba across the Tunari range, 3,050 m, *Brooke 6922* (BM, F, NY). CHUQUISACA: Prov. Tomina, *Weddell 3704 in 1845–1846* (P).

Oenothera elongata has derived one chromosomal complex from *O. longituba*, the second from *O. affinis*. This combination might have originated in southern Bolivia, either through hybridization of the chromosomally homozygous parental species, or by the transmission of a *longituba*-complex through *O. tarijensis* or *O. recurva*, these hybridizing with *O. affinis*. See also the remarks on complex heterozygosity on p. 440.

39. **Oenothera pseudoelongata** Dietrich, sp. nov.—Fig. 160.

Herba annua, erecta, erosulata, simplex vel e basi sursum ramosa, 5–8 dm alta. Plantae dense strigulosae, dense pilis longis brevibusque villosis praeditae, et circum inflorescentiam glanduloso-pubescentes. Folia caulina angustissime elliptica vel lanceolata, acuta, basi acuta vel rotundata, 5–10 cm longa, 0.7–1 cm lata; bractea lanceolata vel anguste ovata, acuta, basi truncata, 2.5–3 cm longa, 0.8–1 cm lata, quam capsula subtenta longiora; folia plana, remote obtuseque vel acute serrata. Inflorescentia simplex vel ramosa. Tubus floralis 5–6 cm longus. Gemmae ambito anguste oblongae vel lanceolatae, 0.8–1.1 cm longae, 3.5–4 mm crassae, saepe rubrae, junctura sepalorum tubo florali rubro-fasciatae; apices sepalorum 2–3 mm longi, erecti vel divergentes. Petala latissime obovata, quam stamina breviora, 0.8–1.3 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 0.9–1.1 cm longum. Capsula 1.5–2.5(–3) cm longa, 3–4 mm crassa. Semina ambito elliptica, 1.5–1.8 mm longa, 0.7–0.8 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, simple or branched from the base upward, 5–8 dm tall. Plants densely strigillose, densely long- and short-villous, and also glandular-pubescent in the region of the inflorescence. Cauline leaves very narrowly elliptic to lanceolate, acute, acute to rounded at the base, 5–10 cm long, 0.7–1 cm wide; bracts lanceolate to narrowly ovate, acute, truncate at the base, 2.5–3 cm long, 0.8–1 cm wide, longer than the capsules they subtend; leaves plane at the margins, remotely serrate, the teeth blunt or sharp. Inflorescence unbranched or branched. Floral tube 5–6 cm long. Buds narrowly oblong to lanceolate in outline, 0.8–1.1 cm long, 3.5–4 mm thick, often flushed with red, red striped at the junction of the sepals with the floral tube; apices of the sepals 2–3 mm long, erect or divergent. Petals very broadly obovate, exceeded in length by the stamens, 0.8–1.3 cm long. Anthers 6–7 mm long, ca. 1 mm broad. Filaments 7–10 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis; 5.5–7 cm long. Stigma lobes 4–5 mm long. Ovary 0.9–1.1 cm long. Capsule 1.5–2.5(–3) cm long, 3–4 cm thick. Seeds elliptic in outline, 1.5–1.8 mm long, 0.7–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Bolivia, Dept. Cochabamba, in fields and along the road from Cochabamba to Todos Santos, 26 km E of Cochabamba, 2,900 m, 3 Apr. 1968, *K. A. Santarius 1989* (MO-2155408, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 233): Known only from the vicinity of Cochabamba in Bolivia.

Specimens examined from cultivated plants:

BOLIVIA. COCHABAMBA: In fields and along the road from Cochabamba to Todos Santos, 26 km E of Cochabamba, 2,900 m, *Santarius 1975**, *1977**, *1980*, *1981*, *1984*, *1988**, *1989**, *1990*, *1991* (DUSS; *1989* also CTES, M; *1975*, *1977*, *1988*, *1989*, *1991* also MO).

Additional specimens examined:

BOLIVIA. COCHABAMBA: Cochabamba, 2,700 m, *Buchtien 2387* (US). Cercado near Cochabamba, 2,600 m, *Steinbach 8730* (BM, GH, K, LIL).

Oenothera pseudoelongata can be distinguished from *O. elongata* by its lower stature, smaller flowers, shorter floral tube, shorter capsules, and larger seeds. Usually it is also more densely pubescent. Its complexes are derived from *O. scabra* and *O. affinis*. As in *O. elongata*, there is evidence here of the exchange of genetic material between the two complexes since the *O. affinis*-like plants derived by crossing *O. affinis* with *O. pseudoelongata* have relatively short and thick capsules.

40. **Oenothera cordobensis** Dietrich, sp. nov.—FIGS. 94–95, 161, 206.

Herba annua, erecta, plerumque er rosulata, simplex vel e basi sursum ramosa, 4–10 dm alta. Plantae dense strigulosae denseque villosae, pilis erectis, praecipue circum inflorescentiam, alibi sparsiore. Folia caulina angustissime elliptica vel anguste elliptica, acuta, basi acuta vel truncata, sessilia, 5–10 cm longa, 1–2 cm lata; bractea lanceloata vel anguste ovata, acuta, basi truncata vel subcordata, sessilia, ad capsulas subtentas subaequalia, apicibus incurvatis, 2–3 cm longa, 0.8–1.5 cm lata; folia valde marginibus undulatis, irregulariter obtuseque serrata. Inflorescentia simplex. Tubus floralis 1.5–2.5 cm longus. Gemmae ambito oblongae, virides, 0.8–1 cm longae, 3–4 mm crassae. Sepala saepe fusco-rubro punctata; apices sepalorum 2–3 mm longi, divergentes. Petala latissime obovata, 1.3–1.5 cm lata. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 0.8–1.2 cm longum. Capsula 1.8–2.5 cm longa, 3–4 mm crassa, extremi valvarum distincti, discreti, crenatique. Semina ambito late elliptica, 1–1.3 mm longa, 0.6–0.8 mm crassa, fusco-rubra punctata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, usually not forming a rosette, unbranched or branched from the base upward, 4–10 dm tall. Plant densely strigillose and densely villous with erect hairs, especially in the region of the inflorescence, and more sparsely so elsewhere. Cauline leaves very narrowly elliptic to narrowly elliptic, acute, acute to truncate at the base, sessile, 5–10 cm long, 1–2 cm wide; bracts lanceolate to narrowly ovate, acute, truncate to subcordate at the base, sessile, subequal in length to the capsules they subtend, the tips incurved, 2–3 cm long, 0.8–1.5 cm wide; leaves strongly undulate at the margins and irregularly serrate with blunt teeth. Inflorescence unbranched. Floral tube 1.5–2.5 cm long. Buds oblong in outline, green, 0.8–1 cm long, 3–4 mm thick. Sepals often flecked with dark reddish brown; apices of the sepals 2–3 mm long, divergent. Petals very broadly obovate, 1.3–1.5 cm long. Anthers 4–6 mm long. Filaments 7–9 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.5–4 cm long. Stigma lobes 4–5 mm long. Ovary 0.8–1.2 cm long. Capsule 1.8–2.5 cm long, 3–4 mm thick, with the ends of the valves free and crenate. Seeds broadly elliptic in outline, 1–1.3 mm long, 0.6–0.8 mm thick, flecked with dark red spots. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: December–April.

Type: Grown from seeds and cultivated in Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Argentina, Prov. Córdoba, Cuesta Blanca near Córdoba, Dec. 1961, *G. Göpel* (MO-2155198, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 227): Known only from a few localities west and south of Córdoba, Argentina.

Specimen examined from cultivated plants:

ARGENTINA. CÓRDOBA: Cuesta Blanca near Córdoba, *Göpel in 1961** (DUSS, M, MO).

Additional specimens examined:

ARGENTINA. CÓRDOBA: Alta Gracia, bank of Arroyo Alta Gracia, 600 m, *Hunziker 1209* (CORD, GH, LIL, RSA), *650* (CORD). Between La Carlota and Canals near San Severo, *Hunziker 11214* (CORD). Between Espinillo and Arroyo Messo near Río Cuarto, *Hunziker 11609* (CORD). Between Pan de Azúcar and Villa Allende near San Chico, *Hunziker 11932* (CORD). Sierra Chica, W slope of Cerro Uritorco, 1,600 m, *Hunziker 18037* (CORD). La Falda, *Hossens 172* pro parte (CORD). Dique, *Kuntze in 1891* (MO, NY).

Experimental hybrids to determine the parentage of *O. cordobensis* have not yet been carried out. Nevertheless, the red-flecked seeds and the absence of a rosette strongly suggest that the *Renneria*-complex might be attributed to *O. tafiensis*, which reaches the southeastern margin of its range in the Sierra de Córdoba. The red-flecked sepals and distinct, crenate valve ends of the capsule suggest *O. longiflora* and *O. ravenii*, the complexes of which are included in *O. parodiana*, frequent in the province of Córdoba.

41. **Oenothera siambonensis** Dietrich, sp. nov.—FIGS. 96–97, 162.

O. mollissima sensu Munz, Physis 11: 282. 1933, pro parte.
O. stricta sensu Munz, Physis 11: 285. 1933, pro parte.
O. parodiana "Siambon" Hecht, Indiana Univ. Publ. Sci. Ser. 16: 277. 1950; Cleland, Jap. J. Genet. 43: 332. 1968.

Herba annua, erecta, erosulata, e basi sursum ramosa, 6–12 dm alta. Plantae dense vel parce strigulosae, dense vel parce pilis longis brevibusque villosis praeditae, et circum inflorescentiam glanduloso-pubescentes. Folia caulina anguste oblonga vel angustissime elliptica ad elliptica, acuta, basi acuta vel rotundata, 4–15 cm longa, 1–3 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi truncata, sessilia, 2.5–3.5 cm longa, 0.5–1 cm lata; folia plana, irregulariter obtuseque serrata. Inflorescentia plerumque simplex. Tubus floralis 3–5.5 cm longus. Gemmae ambito lanceolatae, 1.5–2 cm longae, 3–4 mm crassae, saepe junctura sepalorum tubo florali rubro-fasciatae; apices sepalorum 1.5–3 mm longi, erecti. Petala latissime obovata, 2–2.5 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.2–1.5 cm longum. Capsula 2.5–3 cm longa, 3–4 mm crassa. Semina ambito late elliptica, plerumque fusco-rubro punctata, 1–1.2 mm longa, 0.5–0.6 mm crassa. Numerus gameticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, branched from the ground up, 6–12 dm tall. Plants densely to moderately strigillose, densely to moderately long- and short-villous, and with an admixture of glandular hairs in the region of the inflorescence. Cauline leaves narrowly oblong or very narrowly elliptic to elliptic, acute, acute to rounded at the base, 4–15 cm long, 1–3 cm wide; bracts narrowly lanceolate to lanceolate, acute, truncate at the base, sessile, 2.5–3.5 cm long, 0.5–1 cm wide; leaves plane at the margins, irregularly serrate with blunt teeth. Inflorescence usually unbranched. Floral tube 3–5.5 cm long. Buds lanceolate in outline, 1.5–2 cm long, 3–4 mm thick, often red striped at the junction of the sepals with the floral tube. Sepals yellowish green, sometimes flushed with red; apices of the sepals 1.5–3 mm long, erect. Petals very broadly obovate, 2–2.5 cm long. Anthers 7–8 mm long. Filaments 13–15 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 4–6.5 cm long. Stigma lobes 4–5 mm long. Ovary 1.2–1.5 cm long. Capsule 2.5–3 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, usually flecked with dark reddish brown, 1–1.2 mm long, 0.5–0.6 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Argentina, Prov. Tucumán, edge of fields, Siambón above Tucumán, ca. 985 m, 11 Feb. 1939, *P. A. Munz 15472* (POM, holotype; GH, NY, isotypes).

Distribution (Fig. 240): Elevations of 500–2,000 m in the Argentine provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, and Córdoba.

Specimens examined from cultivated plants:

ARGENTINA. TUCUMÁN: Siambón near Tucumán, *Hecht 196-84** (CTES, DUSS, M, MO). Dry slope in Sierra de San Javier at "Ante Muerta" near Tucumán, *Göpel in 1961** (CTES, DUSS, M, MO). Between Villa Nouges and San Javier near Tucumán, *Göpel in 1961** (CTES, DUSS, M, MO).

Additional specimens examined:

ARGENTINA. JUJUY: Río Chico, *Holmberg in 1908* (SI). San Salvador de Jujuy, *Budín 93* (LIL). San Pablo, *Romero 17* (LIL). SALTA: Alemania near Guachipas, *Venturi 9847* (GH, K). TUCUMÁN: Tafí Viejo, 850 m, *Venturi 37* (LIL), *1325* (US). Above Tucumán, 915 m, *Munz 15465* (POM, US). Villa Nougés, *Munz 15464* (G); *Schreiter 706* (LIL). Siambón, *Lorentz & Hieronymus 753* (CORD, F, G, GOET, NY, POM); *Olea 308* (LIL); *Lillo*

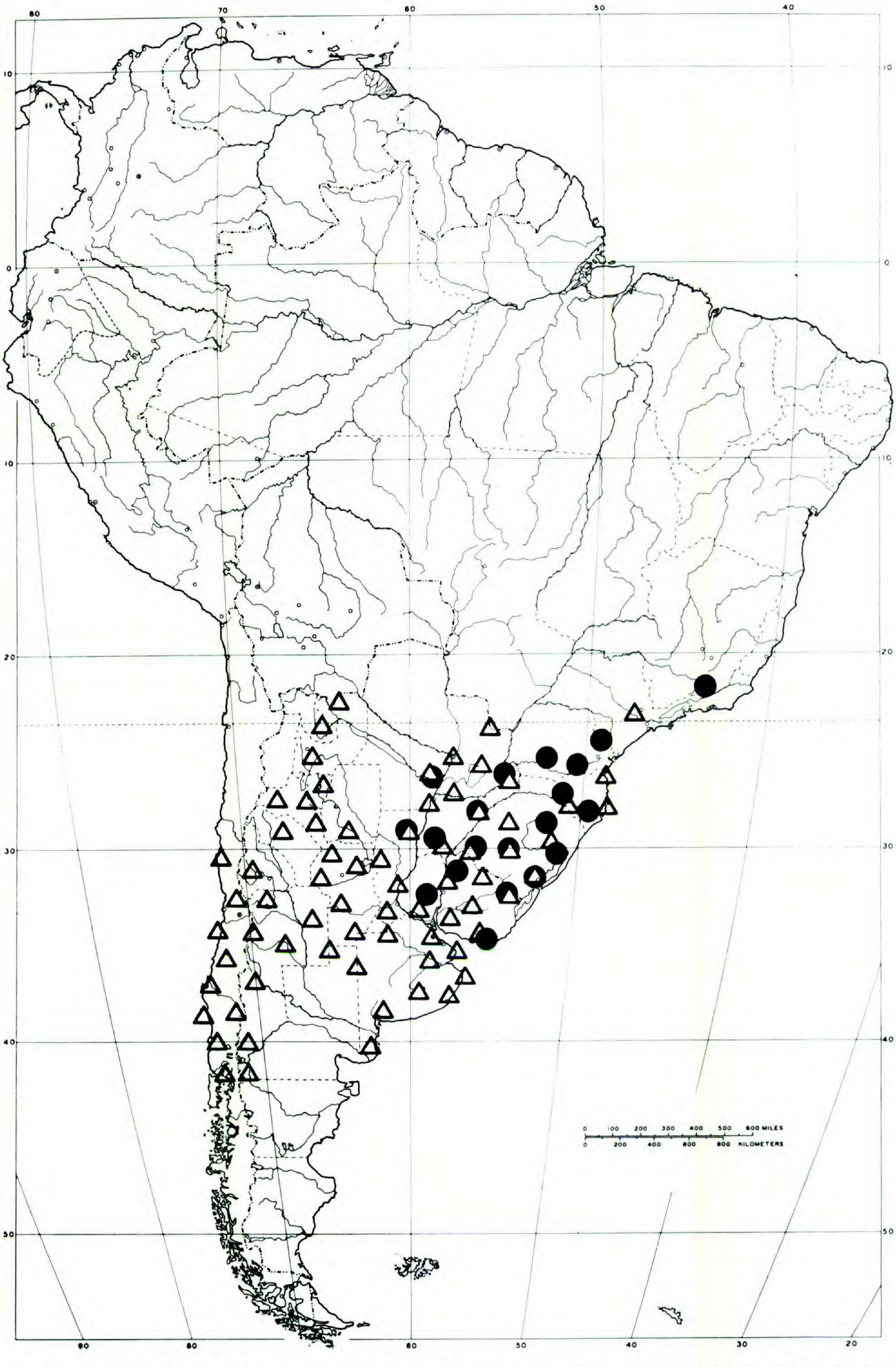


FIGURE 243. Range of homozygous *Oenothera ravenii* subsp. *ravenii* (dots) and as a chromosomal complex in *O. hechtii*, *O. parodiana*, *O. pseudolongiflora*, *O. ravenii* subsp. *argentinae*, *O. ravenii* subsp. *chilensis*, *O. siambonensis*, *O. stricta*, and *O. villaricae* (hollow triangles).

1107 (LIL). Mountains above Siambón, 2,100 m, *Lillo 1772* (LIL). Trancas, 1,950 m, *N.N. 276* pro parte (LIL). Cerro de Campo near Burroyacú, 2,000 m, *Venturi 7748* (MO, POM, SI, US). Las Cuchillas near Burroyacú, 1,100 m, *Lillo 5309, 5310* (LIL). Escaba at Río Chico, 600 m, *Monetti 1665* (GH, LIL). La Cocha at Río Chaco near Cerro del Potrerillo, 700 m, *Bailetti 170* (LIL). CATAMARCA: Dep. Paclin, Balcosna Afuera, 35 km NW of La Merced, 1,300 m, *Hunziker & Di Fulvio 21164* (CORD). El Suncho, *Jörgensen 1440* (LIL, SI). LA RIOJA: Sierra Famatima, La Hoyada, 2,500 m, *Kurtz 15074* (CORD). Sierra Velazco, El Cantadero near La Mina, 2,300–2,400 m, *Hunziker 5219, 5244, 5285* (CORD). CÓRDOBA: La Esquina SE of Cerro Champaquí, *Hunziker 9662* (CORD). Sierra Grande, Copina, *Hunziker 11439* (CORD, RSA), *11437* (CORD). Pampa Achala, 900 m, *Hunziker 11912* (CORD). Sierra Achala, Casas Viejas, *Hieronymus 747* (CORD, F, GOET, US). Luyaba near San Javier, *Castellanos in 1927* (RSA).

The two chromosomal complexes in *O. siambonensis* are derived from *O. scabra* and *O. ravenii*. The latter has long since disappeared from the region where *O. siambonensis* occurs, which suggests that this species may be the oldest complex structural heterozygote resulting from the combination of *O. ravenii* with any other species. It is possible that the populations of *O. siambonensis* that occur in the province of Córdoba, like *O. tucumanensis*, have *O. tafiensis* subsp. *tafiensis* as their *Renneria* element. Since the characteristics of *O. scabra* versus *O. tafiensis* subsp. *tafiensis* are not sufficiently pronounced to make possible the separation of their respective hybrids with *O. ravenii*, however, the separation of *O. siambonensis* into two taxonomic species is a taxonomic impossibility, regardless of the derivation of the various populations grouped here.

42. **Oenothera brevipetala** Dietrich, sp. nov.—FIGS. 100–101, 163.

Herba annua, erecta, erosulata, e basi sursum ramosa, 10–15 dm alta. Plantae dense vel parce pilis brevibus longisque villosis denseque glandulosis praeditae. Folia caulina anguste elliptica, acuta, basi anguste cuneata vel acuta, breviter petiolata, 5–10 cm longa, 1–2 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi acuta vel rotundata, sessilia, 3–4 cm lata, 0.6–1 cm lata, quam capsula subtenta longiora; folia plana, remote obtuseque serrata. Inflorescentia simplex. Tubus floralis 4–4.5 cm longus. Gemmae ambito anguste lanceolatae, 0.8–1 cm longae, 2–3 mm crassae; apices sepalorum ca. 1.5 mm longi, erecti. Petala latissime obovata, 0.6–0.7 cm longa, quam anthera stylumque breviora. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 7–10 mm longum. Capsula 1.3–1.5 cm longa, 3–4 mm crassa. Semina ambito elliptica, 1.1–1.5 mm longa, 0.6–0.7 mm crassa, immaculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, branched from the ground up, 10–15 dm tall. Plants densely to moderately long- and short-villous and densely glandular-pubescent. Cauline leaves narrowly elliptic, acute, narrowly cuneate to acute at the base, short-petiolate, 5–10 cm long, 1–2 cm wide; bracts narrowly lanceolate to lanceolate, acute, acute to rounded at the base, sessile, 3–4 cm long, 0.6–1 cm wide, longer than the capsules they subtend; leaves plane at the margins, remotely serrate, the teeth blunt. Inflorescence unbranched. Floral tube 4–4.5 cm long. Buds narrowly lanceolate in outline, 0.8–1 cm long, 2–3 mm thick; apices of the sepals ca. 1.5 mm long, erect. Petals very broadly obovate, 0.6–0.7 cm long, exceeded in length by the anthers and the style. Anthers 6–8 mm long. Filaments 9–12 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 5–6 cm long. Stigma lobes 4–5 mm long. Ovary 7–10 mm long. Capsule 1.3–1.5 cm long, 3–4 mm thick. Seeds elliptic in outline, 1.1–1.5 mm long, 0.6–0.7 mm thick, not flecked with red. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Bolivia, Dep. Cochabamba, edges of fields near Chacacolloa, ca. 7.5 km NE of Cochabamba, 2,550 m, 30 Mar. 1968, *K. A. Santarius 1972* (MO-2155223, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 234): Known only from the type locality.

Specimens examined from cultivated plants:

BOLIVIA. COCHABAMBA: Edges of fields near Chacacolloa, ca. 7.5 km NE of Cochabamba, 2,550 m, *Santarius 1972**, *1973* (DUSS; *1972* also M, MO).

Additional specimen examined:

BOLIVIA. COCHABAMBA: Liriuni, *Krapovickas 6994* (LIL).

Specimen from plants cultivated in garden:

Botanical Garden of Leningrad, from seeds of Bolivia sent by Cuming in 1847 (LE; as *O. brachypetala* F.M.).

The origin of the chromosomal complexes of *O. brevipetala* is not certain. The absence of strigillose pubescence in this species makes it highly probable that its *Renneria*-complex was derived from *O. scabra*, however, since that is the only species of the subsection in which plants that lack strigillose pubescence occur. *Oenothera indecora* may be the source of the other complex, judging from the small flowers and dense glandular pubescence. On the other hand, this complex might have been derived from *O. affinis* if one had assumed a strong evolutionary trend to small flower size in the complex heterozygote.

43. **Oenothera acuticarpa** Dietrich, sp. nov.—FIGS. 11, 92–93, 164, 207.

Herba annua, erecta, erosulata, e basi sursum ramosa, 7–10 dm alta. Plantae praecipue inferiore dense strigulosae, sparseque pilis longis brevibusque villosis ubique, etiam circum inflorescentiam glanduloso-pubescentibus praeditae. Folia caulina angustissime elliptica vel anguste, lanceolata, acuta, basi anguste cuneata vel acuta, sessilia, 6–15 cm longa, 0.8–2 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi acuta vel rotundata, sessilia, 4–5 cm longa, 0.8–1 cm lata; folia plana, irregulariter serrata. Inflorescentia simplex. Tubus floralis 4–6 cm longus. Gemmae ambito anguste oblongae vel lanceolatae, flavidae, junctura sepalorum tubo florali rubro-fasciatae, 1.5–2 cm longae, 4–5 mm crassae; apices sepalorum 1–2 mm longi, erecti. Petala latissime obovata, 1.8–2.5 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.5–1.8 cm longum. Capsula 2.5–3.5 cm longa, 3–4 mm crassa, in acuminem abrupte decrescens. Semina ambito elliptica, fusco-rubro punctata, 1–1.2 mm longa, 0.5–0.6 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, branched from the ground up, 7–10 dm tall. Plants densely strigillose, especially below, and sparsely long-villous and densely short-villous elsewhere, with a dense admixture of glandular pubescence in the inflorescence. Cauline leaves very narrowly elliptic to narrowly lanceolate, acute, narrowly cuneate to acute at the base, sessile, 6–15 cm long, 0.8–2 cm wide; bracts narrowly lanceolate to lanceolate, acute, acute to rounded at the base, sessile, 4–5 cm long, 0.8–1 cm wide; leaves plane at the margins, irregularly toothed. Inflorescence unbranched. Floral tube 4–6 cm long. Buds narrowly oblong to lanceolate in outline, yellowish, red striped at the junction of the sepals with the floral tube, 1.5–2 cm long, 4–5 mm thick; apices of the sepals 1–2 mm long, erect. Petals very broadly obovate, 1.8–2.5 cm long. Anthers 9–11 mm long. Filaments 18–24 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 5.5–8 cm long. Stigma lobes 4–7 mm long. Ovary 1.5–1.9 cm long. Capsule 2.5–3.5 cm long, 3–4 mm thick, narrowed to an obvious point at the end (Fig. 11). Seeds elliptic in outline, flecked with dark reddish brown, 1–1.2 mm long, 0.5–0.6 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 10 and 2 bivalents* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Argentina, Prov. Tucumán, Villa Nougés near Tucumán, Dec. 1961, *G. Göpel* (MO-2155221, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 239): Known only from the type locality.

Specimen examined from cultivated plants:
ARGENTINA. TUCUMÁN: Villa Nougés near Tucumán, *Göpel in 1961** (DUSS, M, MO).
Additional specimen examined:
ARGENTINA. TUCUMÁN: Villa Nougés, *Pastore in 1916* (SI-4670).

The analysis of the chromosomal complexes of *O. acuticarpa* is simple. On self-pollination, homozygous individuals of *O. tafiensis* subsp. *parviflora* segregate in the progeny. The second complex is derived from *O. affinis* and F_1 hybrids between *O. affinis* and *O. acuticarpa* comprise two classes of plants, one identical to each of the parents. *Oenothera affinis* does not, however, appear in the selfed progeny of *O. acuticarpa*.

The strain of *O. acuticarpa* cultivated in Düsseldorf consistently forms a ring of 10 and 2 bivalents at meiotic metaphase I. Evidently the two free *Renneria* chromosomes are responsible for segregation of homozygous individuals and so for the failure of this species to become a complete complex heterozygote.

44. **Oenothera tucumanensis** Dietrich, sp. nov.—FIGS. 98–99, 165.

O. indecora sensu Munz, Physis 11: 281. 1933, pro parte; Amer. J. Bot. 22: 658. 1935, pro parte.

Herba annua, erecta, erosulata, simplex vel e basi sursum ramosa, 5–10(–13) dm alta. Plantae praecipue inferiore dense strigulosae, interdum sparse pilis longis praeditae, omnino pilis brevibus glandulosisque praeditae. Folia caulina angustissime elliptica vel elliptica, acuta, basi anguste cuneata vel acuta, plerumque breviter petiolata, 4–10 cm longa, 0.7–2 cm lata; bractea angustissime elliptica vel anguste lanceolata, acuta, basi acuta, plerumque sessilia, raro breviter petiolata, 3–5 cm longa, 0.5–1 cm lata, quam capsula subtenta longiora; folia plana vel marginibus manifeste undulatis, irregulariter obtuseque serrata. Inflorescentia plerumque ramosa. Tubus floralis 1.3–2.5 cm longus. Gemmae ambito oblongae vel lanceolatae, 0.6–0.9 cm longae, 2–3 mm crassae, flavo-virentes; apices sepalorum 1.5–2 mm longi, erecti vel divergentes. Petala latissime obovata, 0.5–1 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.2–1.5 cm longum. Capsula 1.5–2.5 cm longa, 2–2.5 mm crassa. Semina ambito elliptica, 1–1.2 mm longa, 0.5–0.6 mm crassa, immaculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, simple or branched from the base upward, 5–10(–13) dm tall. Plants densely strigillose, especially below, sometimes sparsely long-villous, and short-villous and glandular-pubescent through-

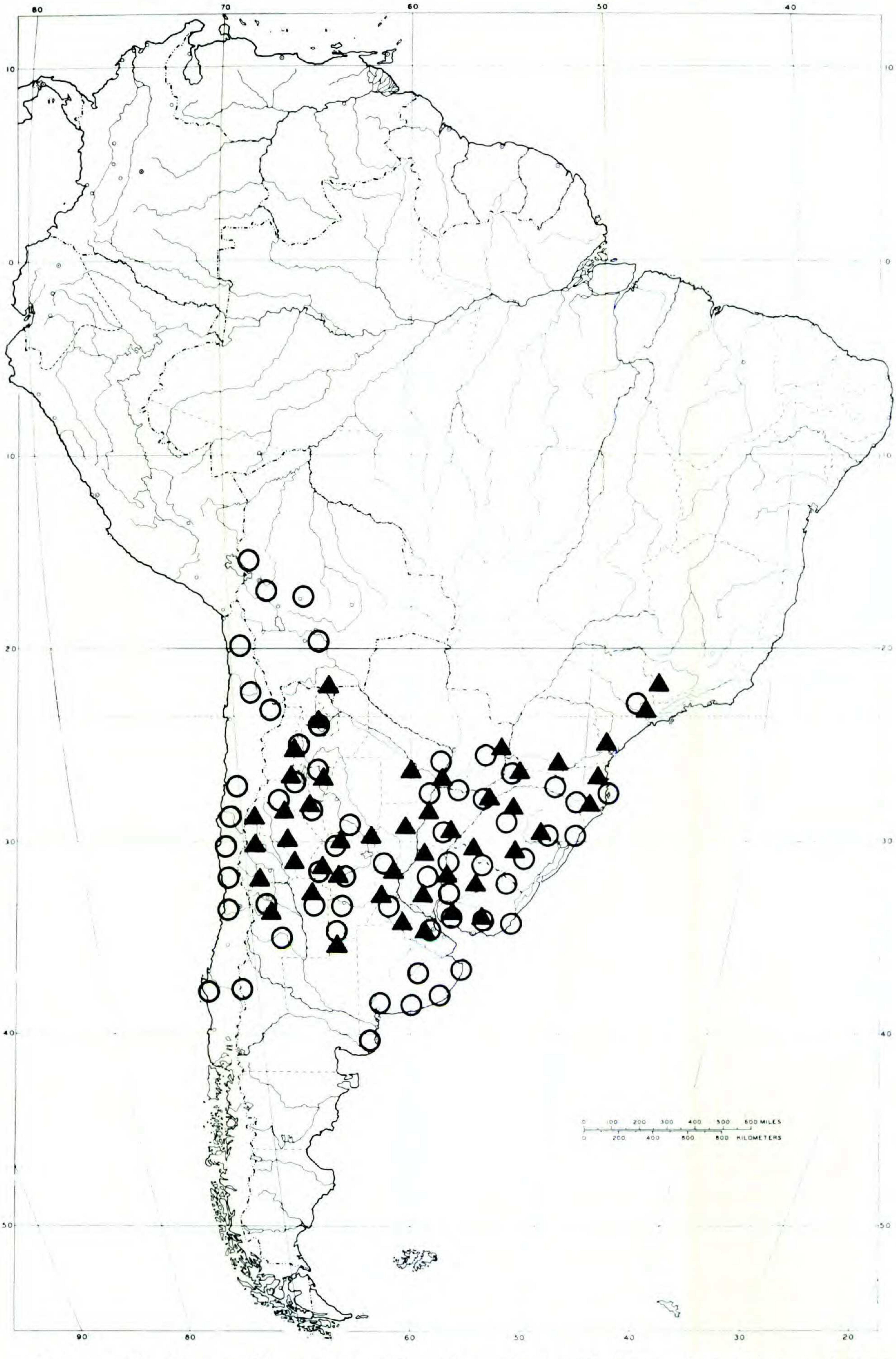


FIGURE 244. Range of homozygous *Oenothera affinis* (filled triangles) and as a chromosomal complex in *O. acuticarpa*, *O. elongata*, *O. mollissima*, *O. montevidensis*, *O. parodiana* subsp. *brasiliensis*, *O. picensis*, *O. pseudoelongata*, and *O. pseudolongiflora* (circles).

out. Cauline leaves very narrowly elliptic to elliptic, acute, narrowly cuneate to acute at the base, usually short-petiolate, 4–10 cm long, 0.7–2 cm wide; bracts very narrowly elliptic to narrowly lanceolate, acute, acute at the base, usually sessile, rarely short-petiolate, 3–5 cm long, 0.5–1 cm wide, longer than the capsules they subtend; leaves plane or evidently undulate along the margins, irregularly bluntly toothed. Inflorescence usually branched. Floral tube 1.3–2.5 cm long. Buds oblong to lanceolate in outline, 0.6–0.9 cm long, 2–3 mm thick, yellowish green; apices of the sepals 1.5–2 mm long, erect or divergent. Petals very broadly obovate, 0.5–1 cm long. Anthers 3–5 mm long. Filaments 4–8 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.7–3.5 cm long. Stigma lobes 2–4 mm long. Ovary 1.2–1.5 cm long. Capsule 1.5–2.5 cm long, 2–2.5 mm thick. Seeds elliptic in outline, 1–1.2 mm long, 0.5–0.6 mm thick, not flecked with red. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: September–May.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Argentina, Prov. Tucumán, in the rubble of the Río Salí near bridge on Ruta 9, E of Santa María de Tucumán, 420 m, 3 Mar. 1968, *K. A. Santarius 1657* (MO-2155219, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 236): At elevations from 400 to 2,000 m in the Argentine provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja and Córdoba.

Specimens examined from cultivated plants:

ARGENTINA. TUCUMÁN: In the rubble of the Río Salí near bridge on Ruta 9, E of Tucumán, 420 m, *Santarius 1657**, *1664** (DUSS; *1657* also M, MO). Dry river bed between Villa Nougés and San Pablo near Tucumán, *Göpel in 1961** (DUSS).

Additional specimens examined:

ARGENTINA. JUJUY: Sierra de Calilegua, Ledesma, 700 m, *Venturi 5247* (LIL, SI, US). Three km S of San Salvador de Jujuy, 1,200 m, *Eyerdam et al. 22409* (GH, UC); *Arnow 3646* (MO). SALTA: Vicinity of Pampa Grande, *Nelson 12578* (CORD). TUCUMÁN: San Miguel de Tucumán, 450 m, *Lillo 8604* (F, LIL, MO, UC), *2066* (F, US), *474*, *844*, *912* (LIL); *Schreiter 1874*, *2168*, *3238* (LIL); *Meyer 12227* (RSA). Río Salí near Tucumán, 450 m, *898a* (BAA, US). Yerba Buena, *Wall in 1946* (S); *Sparre 480* (S); *Lillo 13248* (LIL); *Schreiter 1592* (LIL). Cruz Alta, 400 m, *Bailetti in 1917* (GH, LIL). Siambón, ca. 1,000 m, *Munz 15472* (NY). El Timbo near Burroyacú, 600 m, *Venturi 2231* (BM, LIL). Between Tafí Viejo and Muñecas, 600 m, *Schreiter 1879* (LIL). Monteros, León Rongues, *Herrera 578* (LIL). Sierra del Aconquija, *Humbert 10915* (P). CATAMARCA: Andalgala, *Jörgensen 1054* pro parte (GH, LIL, MO, SI, US); *Schickendantz 128* (B, destroyed, F photograph, POM, SI). City of Catamarca, *Picinnini 68205* (BAB); *Castillon in 1910* (SI-26724). Yacutula near Belén, *Schickendantz in 1887*, *1879* (CORD); *White 18* (BM). Dep. El Alto, at Ruta 64 near El Portezuelo, *Sublis & Artico 53* (CORD). Dep. Ambato, El Rodeo, 1,800 m, *N.N. in 1949* (LIL-315929, LIL-318578). Belén, between Quebrada de los Potrerillos and El Rodeo, 2,700 m, *Sleumer & Vervoorst 2472* (LIL). Dep. Santa María, between the rivers, 2,000 m, *Peirano in 1933* (GH, LIL). LA RIOJA: Sierra Velasco, Yacuchi, *Kurtz 15415* (CORD). CÓRDOBA: Dep. Punilla, La Falda, *Kurtz 10167* (CORD).

Judging from the fact that *O. peduncülifolia* × *O. indecora* subsp. *bonariensis* produces plants that are phenotypically very similar to *O. tucumanensis*, these are its parents. This species therefore provides an example of a complex heterozygote that arose in the presence of its two parents, and still grows together with them. The plants from Córdoba might have originated following hybridization between *O. tafiensis* subsp. *tafiensis*, which occurs in the mountains of Córdoba, and the widespread *O. indecora*. Notwithstanding this possibility, they are indistinguishable from the type and it is therefore not possible to regard them as a distinct species taxonomically.

45. **Oenothera punae** Kuntze, Rev. Gen. Pl. 3(2): 99. 1893.—Figs. 84–85, 166, 184, 208.

Onothera kuntziana H. Lév., Monogr. Onoth. 359. 1909; Bull. Acad. Int. Géogr. Bot. 19: 319. 1909, illeg. subst. for *O. punae* Kuntze.
Raimannia punae (Kuntze) Sprague & Riley, Bull. Misc. Inform. 1921: 201. 1921.
Oenothera nana sensu Munz, Physis 11: 280. 1933, pro parte; Amer. J. Bot. 22: 650. 1935, pro parte.
O. nana sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 539. 1941, pro parte.

Annual to perennial herb, forming a rosette, with a prostrate main stem and prostrate branches arising from the rosette, the main stem rarely obliquely arising from the ground, the branches 5–25 cm long. Plants exclusively densely strigillose. Rosette leaves linear to very narrowly elliptic, acute, narrowly cuneate at the base, short-petiolate, 2–5 cm long, 1–3(–5) cm wide; cauline leaves linear to very narrowly elliptic, acute, narrowly cuneate at the base, sessile, 1.5–4 cm long, 1–3(–5) cm wide; bracts linear to very narrowly elliptic, acute, narrowly cuneate to acute at the base, sessile, 1.5–3(–4) cm long, 1–3(–5) cm wide; leaves plane or evidently undulate at the margins, irregularly bluntly toothed. Inflorescence unbranched. Floral tube 5–10(–15) mm long; buds oblong to broadly elliptic in outline, green or yellowish green, often red striped at the junction of the sepals with the floral tube, 3–4 mm long, 2–3 mm thick. Sepals often flecked with dark red; apices of the sepals 0.5–1 mm long, mostly erect. Petals very broadly obovate, often flushed with red, 0.4–1 cm long. Anthers 2.5–4 mm long. Filaments 2.5–6 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 0.8–1.5(–2) cm long. Stigma lobes 1.5–2 mm long. Ovary 5–10 mm long. Capsule 1.2–1.7 cm long, 2.5–3.5 mm thick, cylindrical or slightly enlarged towards the base. Seeds broadly elliptic to rotund in outline, 0.8–1.2 mm long, 0.7–0.9 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: Northern area, October–March; southern area, November–April.

Type: Bolivia, Dep. Oruro, at the Challapata railroad station on high plateau of Puno, 11 Mar. 1892, *O. Kuntze* (not located).

Distribution (Fig. 238): At elevations from 2,000 to 4,700 m in the Andes; in the southern departments of Peru, including Cuzco, Arequipa, and Puno; in the departments of La Paz, Cochabamba, Oruro, Potosí, and Tarija in Bolivia, but not yet seen from Chuquisaca; and in the provinces of Jujuy, Salta, Tucumán, Catamarca, and La Rioja in Argentina.

Specimens examined from cultivated plants:

Peru. puno: Waste places ca. 2 km SE of Zepita, sandy soil, 3,820 m, *Santarius 2034** (DUSS, M, MO). Dry grasslands, ca. 6 km NNW of Puno, below road to Juliaca, 3,850 m, *Santarius 2041**, *2042** (DUSS; *2041* also MO). Sandy slopes above Chimu, ca. 8 km SE of

Puno at the road to Chucuito, 3,900 m, _Santarius 2044_* (DUSS, M, MO); 4,000–4,100 m, *Santarius 2046, 2047, 2048, 2055* (DUSS; *2046* also M; *2046, 2048* also MO).

BOLIVIA. LA PAZ: La Paz, dry slopes of the Cerro Calvario ca. 100 m N of the chapel, 3,800 m, _Santarius 2008–2012, 2013_*, _2014_*, _2015_* (DUSS; *2008* also CTES, M; *2008, 2010, 2012–2015* also MO). COCHABAMBA: Ca. 35 km E of Cochabamba on the road to Todos Santos, dry grasslands, 3,000 m, _Santarius 1997_*, _2000_, _2001_*, _2002_* (DUSS; *2001, 2002* also MO).

ARGENTINA. JUJUY: Steppe ca. 1 km S of Abra Pampa, ca. 100–150 m W and NW of the cemetery, 3,485 m, *Santarius 1886* (DUSS, MO). On sandy rubble in the steppe along road from La Quiaca to Yaví, ca. 3 km E of La Quiaca, 3,550 m, *Santarius 1888, 1898* (DUSS). TUCUMÁN: Rubble in bed of Río Angostura ca. 5 km N of Tafí del Valle, 2,000–2,550 m, _Santarius 1742_*, _1743_ (DUSS, MO; *1742* also CTES, M).

Representative specimens examined:

PERU. AREQUIPA: Prov. Condesuyos, Chuquibamba, 3,800 m, *Stafford 1178* (BM). CUZCO: Prov. Anta, El Chaccan near Cillapuyu, 3,605 m, *Brunel 240* (MO). PUNO: Puno, 4,000 m, *Soukup 105* (F). Arapa near Azángaro, 3,900 m, *Aguilar 222, 225* (USM). Conima near Huancané, 3,900 m, *Aguilar 224* (USM). Moho near Huancané, *Aguilar 226* (USM). Amantani near Lake Titicaca, 3,900 m, *Aguilar 229, 233* (USM). Juliaca, 4,250 m, *Stafford 271* (K). Macusani near Carabaya, 4,360 m, *Vargas 7126* (MO, RSA). Lake Titicaca, 3,820 m, *Vargas 1275* (F). Cayachita, 4,450 m, *Sharpe 14* (K). Huascapata, 3,900 m, *Aguilar 223* (USM).

BOLIVIA. LA PAZ: Mountain slopes near La Paz, 3,800 m, *Buchtien 644a* (GH, NY, US). La Paz, *Wolsterholme 9* (K). Cerro Calvario near La Paz, 3,800 m, *Parodi 10107* (BAA, POM), *10120* (MO). Prov. Larecaja, road to Coroico, 4,000 m, *Mandon 631* (G, K, NY, P, S, W). Prov. Ingari, Hacienda San José on peninsula Taraco, *Hammarlund 164* (S). Laja, *Hill 158* (K). Above Guaqui, *Hill 159* (K). Hills near Huatajata at Lake Titicaca, 4,000 m, *Heine in 1954* (M). Calachaca W of Pucarani, 3,900 m, *Herzog 2474a* (L). Upper Araca valley near Viloco, 3,800 m, *Herzog 2334b* (L). Pacajes: Corocoro, 4,000 m, *Asplund 2420* (UPS). ORURO: Cona Cona station on the line from Oruro to Cochabamba, 4,250 m, *Brooke 5214* (BM). 141 mi from La Paz, 3,950 m, *Brooke 5254* (BM). Challapata, 3,900 m, *Asplund 5972* (US). Prov. Cercado, Hacienda Huancaroma near Eucaliptus, 3,800 m, *Hammarlund 119, 120* (S). Viloco, 100 mi from Oruro, road to Eucaliptus and Cascata near Araca, *Brooke 5329A* (BM). POTOSÍ: 4,000 m, *Cardena 125* (GH). Uyuni, 4,000 m, *N.N.* (S). TARIJA: Escayache near Tarija, *Fiebrig 3030* (BM, F, GH, K, LD, LE, LIL, NY, S, SI, US). Department unknown: Between Quebrada Honda and Salitre, 4,000 m, *Fries 1028* (S).

ARGENTINA. JUJUY: Cerro Negro near Yaví, 4,000 m, *Meyer 33730* (LIL). San Gregorio near Tilcara, 3,400 m, *Sleumer 3133* (LIL). Laguna Tres Cruces near Cochinoca, 3,700 m, *Claren in 1901* (CORD, S). La Rinconada, 3,800 m, *Claren in 1901* (CORD, S). Cajas, 35 km E of La Quiaca, 3,900 m, *Hjerting et al. 123* (C). Mina Águilar, 4,700 m, *Schwabe 558* (BAA), 4,300 m, *452, 471* (BAB); *Petersen & Hjerting 116* (C, LIL); *Cabrera & Frangi 20713* (LP); *Cabrera 9223* (LP). Quebrada de Cajos near Yaví, 4,000 m, *Cabrera 7845* (LP). SALTA: Lizoite near Sta. Victoria, 3,340 m, *Meyer & Bianchi 33738, 33739* (LIL). Top of Obispo near Cachi, 3,720 m, *Rosmero in 1947* (LIL). Between Trancas and Cafayate, *Haumann 31-1521* (BA). Banks of Río Colorado near Cafayate, *Krapovickas & Cristóbal 20686* (CTES). TUCUMÁN: Tafí, 2,200 m, *Lillo 4315, 7779* (LIL), *7500* (GH, LIL, UC); *Rodriguez 302* (GH, LIL, SI). Lara at Cerro Calchaquies, *Baer 10* (LIL, POM). La Ciénaga, 2,500 m, *Lillo 4034, 4072, 1212* (LIL); *Lorentz & Hieronymus* (CORD, GOET). Río Blanco near Cerro Muñoz, 2,500 m, *Lillo 3034, 8867* (LIL). Mesopotamia, *Castillon 182, 2262* (LIL). La Puerta, 4,000 m, *Parodi 10812* (POM). Cuesta de los Cordones, 3,800 m, *Schreiter 7059* (LIL, MO); *Burkart 5337* (POM, SI). Tafí del Valle, 2,000 m, *Sparre 5648* (LIL); *Araque & Barkley 19AR162* (F, LIL); *Wall in 1946* (S); *Dinelli 21518* (BAB); *Sleumer 146* (B, LIL). Río Churqui, 2,000 m, *Lillo 7655* (LIL). Infiernillo, 3,500 m, *Sparre 6032* (LIL); *Hjerting et al. 9284* (C); *Sparre 1094* (S); *Burkart 22081* (SI); *Cristóbal 523* (LIL, UC); *Krapovickas & Cristóbal 20506* (CTES); *Krapovickas et al. 21851* (CTES, MO). Chorro near Trancas, 4,000 m, *Schreiter 663* (LIL). CATAMARCA: Portezuelo de Yutiyaco, Cerro del Campo Grande, *Schickendantz 315* (CORD, GOET). Capillitas, *Schickendantz* (CORD). Sierra de Ambato, El Rodeo to Casa de Cubas at Cerro Manchado, 3,300–3,400 m, *Hunziker & Di Fulvio 19803, 19918* (CORD). Dep. Sta. María, Sierra de Aconquija, 3,100 m, *Peirano in 1933* (LIL-80204). LA RIOJA: Sierra de Famatima, Vallecito, *Hieronymus & Niederlein 713* (CORD). La Encrucijada, *Hieronymus & Niederlein 481* (CORD). Portezuelo del Caño de Tocino, 3,350 m, *Krapovickas & Hunziker 5303* (BAB, CORD). Puerto Sta. Rosa, 3,100 m, *Hunziker 1885* (CORD, POM). Mesada de Casablanca, *Krapovickas & Hunziker 5262* (BAB, CORD). Top of Espíritu Santo, *Jiménez 15243* (CORD). Mina San Juan, 3,050–3,200 m, *Kurtz 13590* (CORD). El Volcán, *Kurtz 14653* (CORD, MO). La Batea, 2,900 m, *Hunziker 1861* (CORD).

Oenothera punae provides a classical example of our often fragmentary knowledge of plant distributions in the high Andes. It is collected time and time again along the Andean highways, but very seldom in the vast tracts of land that lie between. It is, for example, inconceivable that the species should be absent in the department of Chuquisaca, Bolivia. Also, the very few collections available from southern Bolivia (*Fiebrig 3030*) clearly do not provide an accurate indication of the true situation. Perhaps the scanty representation of *O. punae* in herbaria is also related to the small flowers and generally inconspicuous nature of this species.

As in the other highly condensed Andean species of the subsection, *O. nana*, *O. punae* has complexes from at least three species of series *Renneria*: *O. peruana*, *O. versicolor*, and *O. lasiocarpa*. These are in *O. punae* combined with a genome derived from *O. indecora* subsp. *boliviensis* of series *Allochroa*. One striking fact is that the glandular pubescence of *O. indecora* is completely absent in *O. punae*.

In populations of *Oenothera nana* and *O. punae* it is possible to catch a glimpse of the very active and rapidly evolving relationship between these two taxa. They frequently grow together, and progenies from seeds taken from a single plant in the wild often consist of two or even three distinct and sharply delimited sorts of plants. Either of the *Renneria* complexes found in *O. nana* may be present interchangeably in *O. punae*. If one designates the *nana*-complexes respectively *Ra* and *Rb*, and the *indecora*-complex of *O. punae C*, the following genetic constitutions were recognized among the collections made by Professor Santarius:

Santarius 1886—Ra–Rb + Ra–C + Rb–C
Santarius 1888—Ra–Rb + Rb–C
Santarius 1997— Ra–C + Rb–C
Santarius 2001—Ra–Rb + Ra–C + Rb–C
Santarius 2008— Ra–C + Rb–C
Santarius 2010— Ra–C + Rb–C
Santarius 2012— Ra–C + Rb–C
Santarius 2013— Ra–C + Rb–C
Santarius 2014— Ra–C + Rb–C
Santarius 2055—Ra–Rb + Rb–C

Voucher specimens documenting these results are deposited in the Herbarium of the Botanisches Institut at the University of Düsseldorf (DUSS). Among the herbarium material I have examined from other institutions, the following combinations are also represented:

Fiebrig 3030 (US)— Ra–Rb + Rb–C
Fries 1028 (S)— Ra–Rb + Ra–C
Hammarlund 119 (S)—Ra–Rb + Rb–C

The two different sorts of *O. punae* can be distinguished by the shape of their mature capsules. In the first, the capsules are cylindrical, whereas in the second, they are somewhat broadened at the base and usually also somewhat shorter. It is however not desirable to separate them taxonomically as independent species owing to their great similarity and close genetic relationships as well as to the presence of intermediate plants.

These facts can only be interpreted to indicate a tendency for the exchange of genomes between species growing together, as has already been noted from *O. sandiana* and *O. parodiana.* Evidently the system is balanced so that all combinations give a ring of 14 chromosomes at meiotic metaphase I, since no plants with smaller rings have been detected among the progenies that have been cultivated so far.

In such a system, crossing over can lead to the exchange of genes between more than two distinct genomes, a system of high evolutionary potential in enhancing the variability of the overall population and hence its capacity to produce new recombinants in response to the selective pressures of the extreme environments where these plants grow.

B. Subsection RAIMANNIA

Oenothera sect. **Oenothera** subsect. **Raimannia** (Rose) Dietrich, stat. nov. Based on *Raimannia* Rose, Contr. U.S. Natl. Herb. 8: 330. 1905. TYPE: *Oenothera laciniata* Hill.

Oenothera subgen. *Raimannia* (Rose) Munz, Amer. J. Bot. 22: 645. 1935; N. Amer. Fl., ser. 2, 5: 104. 1965, pro parte.

This is a primarily North American group of approximately eight species. Only one species, *Oenothera laciniata,* reaches South America. The description and full synonymy for this subsection will be given in connection with a forthcoming revision of the group as a whole.

46. **Oenothera laciniata** Hill, Hort. Kew. 172/4, *tab. 6.* 1768.

A complete description of this species is not given here, pending the completion of current investigations of the species of subsect. *Raimannia.*

Type: From the Carolinas, cultivated at the Royal Botanic Gardens, Kew (BM? Not seen).

KEY TO THE SUBSPECIES

1. Sepal tips 0.1–1 mm long, erect .... 46a. subsp. *pubescens*
1'. Sepal tips 1–2 mm long, more or less spreading .... 46b. subsp. *laciniata*

46a. **Oenothera laciniata** subsp. **pubescens** (Willd. ex Spreng.) Munz, North Amer. Fl., ser. 2, 5: 109. 1965; Opera Bot., Ser. B, 3: 40. 1974.—FIGS. 167, 191–192.

O. pubescens Willd. ex Spreng., Syst. Veg. 2: 229. 1825.

O. stuebelii Hieron., Bot. Jahrb. Syst. 21: 327. 1895. TYPE: Ecuador, Prov. Imbabura, Loma and vicinity of La Canaballa, 2,000–2,300 m, 1 July 1871, *A. Stübel 161 b* (B, destroyed, F-14013 photograph).

O. laciniata sensu Munz, Contr. Gray Herb. 75: 20. 1925.

O. laciniata var. *nocturna* (Jacq.) Munz, Amer. J. Bot. 22: 656. 1935, pro parte.

O. laciniata var. *pubescens* (Willd.) Munz, Amer. J. Bot. 22: 656. 1935.

O. verrucosa Munz, Amer. J. Bot. 22: 657. 1935, pro parte.

O. pennellii Munz, Leafl. West. Bot. 2: 156. 1939. TYPE: Mexico, Nuevo León, Sierra Madre Oriental, from grassy slope, Mt. "El Infiernillo," Pablillo, southeast of Galeana, 29 June 1934, *F. W. Pennell 17139* (US-1640419).

Plants annual to perhaps perennial, erect, forming a rosette, unbranched or few to many branched from the base, 0.5–5 dm tall; side branches from the rosette prostrate to arcuate-ascending. Plants densely to very sparsely strigillose and densely to sparsely villous, very sparsely to sparsely glandular-pubescent only on the sepals and floral tube. Rosette leaves narrowly oblanceolate, acute, gradually narrowed to the petiole, 5–10 cm long, 0.5–1 cm wide; cauline leaves very narrowly elliptic to lanceolate or narrowly oblanceolate, acute, the base truncate to subcordate, sessile or short-petiolate, 3–8 cm long, 0.5–1.5(–2.5) cm wide; bracts narrowly lanceolate to lanceolate, acute, attenuate to truncate at the base, sessile or short-petiolate, 2.5–6 cm long, 0.5–1.5(–2) cm wide; all leaves deeply sinuate-toothed to subentire, plane to prominently undulate at the margins. Inflorescence simple or branched; flowers erect, the mature buds nodding, the younger ones erect. Floral tube 2–3.3 cm long. Buds narrowly oblong to oblong in outline, yellowish green, red striped at the zone of attachment of the sepals, often generally flushed with red and flecked with reddish brown, 5–15 mm long, 3–5 mm wide; sepal tips 0.1–1 mm long, erect. Petals broadly obovate to very broadly obovate, yellow, 5–15 mm long. Anthers 3–9 mm long. Filaments 6–12 mm long. Style 2.8–4 cm long, the lobes of the stigma 2.5–5 mm long; style surrounded by the anthers at anthesis, these shedding pollen directly on it. Ovary 1–2 cm long. Capsule (2–)3–4 cm long, 2.5–4 mm thick, arising from the stem at an acute angle, straight or curved; valves of the capsule curved outward following dehiscence. Seeds broadly elliptic to rotund in outline, 0.9–1.3 mm long, 0.6–1 mm thick, brown. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 12 and 1 bivalent** at meiotic metaphase I). Flowering time: throughout the year. (The description is based exclusively on South American plants.)

Type: Ecuador, *A. von Humboldt*, Herb. Willdenow 7177 (B, holotype, F-14008 photograph).

Distribution (Fig. 238): Andes of Colombia, Ecuador and Peru south to the province of Junín, elevation 2,000–3,900 m; in North America from Western Texas to Arizona south to Guatemala.

Specimens examined from cultivated plants:

PERU. JUNÍN: Valley of Río Mantaro, stony places between the river and the railway ca. 1 km S of the station of Pachacayo, ca. 45 km S of La Oroya, ca. 3,650 m, *Santarius 2190**, *2191**, *2192**, *2195**, *2196**, *2197**, *2198**, *2200**, *2202** (DUSS; *2190*, *2198* also MO; *2190* also CTES). AYACUCHO: Waste places and slopes W of Ayacucho, ca. 2,900 m, *Santarius 2235**, *2236**, *2237**, *2238*** (DUSS; *2235* also MO). LIMA: Rimac valley, between Matucana and Surco, on road and dry slopes between km 74.9 and 76.1, ca. 2,200 m, *Santarius 2326** (DUSS).

Additional South American specimens examined:

COLOMBIA. CUNDINAMARCA: Facacativá, 2,650 m, *Schneider 1007* (S). Usaquén, 2,650 m, *Schneider 340* (S). VALLE: Río Bugalagrande, from La Parilla to La Machuca, Loma of Barragán, 2,660–2,750 m, *Cuatrecasas 20704* (F). NARIÑO: "La Chorrera," 2,600 m, *Fernández & Mora 1217* (NY). Pasto, Botanical Garden of the University, 2,900 m, *Porter 1042* (GH). Without exact locality: Nova Grenada, *Triana in 1851–1857* (US).

ECUADOR. CARCHI: Tulcán, 2,700 m, *Harling 4028* (S, UPS). IMBABURA: Lake Cuicocha, *Summers 821* (F, GH); *Prescott 218* (NY). Hacienda "Rosa Pamba" near Otavalo, 2,850–3,000 m, *Solís 8028* (F). PICHINCHA: Guápulo near Quito, 2,650 m, *Asplund 6284* (G, K, LD, NY, P, R, UPS, US). Vicinity of Quito, 2,800 m, *Solís 1529* (M), *10039* (F); *Hall 1* (K); *Benoist 2107, 4303* (P); *Couthouy in 1855* (GH, NY); *Karsten* (LE). Lake Magdalena near Quito, *Hartweg 982* (BREM, G, K, LD, NY, P). Nayón, *Benoist 2616* (P). Puéllaro, 2,100 m, *Solís 16492* (F). Valley of Tumbamba, Quebrada del Machángara, 2,800 m, *Firmín 67* (F, US). W of Nono, 2,700 m, *Harling et al. 10248* (RSA). El Llalo, ca. 3,650 m, *Balls 5841* (K). NAPO: Paluquillo near Papallacta, Cerro Antisana, *Grubb et al. 190* (NY). COTOPAXI: Plateau of Latacunga and vicinity of Volcán Cotopaxi, ca. 2,250 m, *N.N. in 1858* (M). Volcán Cotopaxi, 2,800–3,500 m, *N.N. in 1858* (M). TUNGURAHUA: 10 km S of Mocha, 3,300 m, *Harling et al. 6892* (RSA). Between Leito and La Cima, 2,700–3,000 m, *Solís 9020* (F). Between Casingana and Chilcaloma, 2,900–3,300 m, *Solís 9104* (F). BOLÍVAR: Between Guaranda and Vinchoa, 2,800 m, *Solís 5959* (F). CHIMBORAZO: Sandy plains near Riobamba, 2,900 m, *Rimbach 420* (F, NY, S, UC); *Spruce 5039* (C, LE, G, GH, K, LD, P); *Rivet 142, 149* (P). Valley of Puaranda, S of Chimborazo, 2,500–2,900 m, *Wagner 3* (M). El Carmén near Sibambe, 2,450 m, *Solís 5551* (F). Javiñac, ca. 15 km from Penipe, 2,800 m, *Lugo 555* (RSA). Slopes of Cerro Chiguazo, 2,900 m, *Lugo 509* (RSA). El Retén, 20 km S of Cebades, 3,200 m, *Harling et al. 6618* (RSA). CAÑAR: Tambillo, 2,785 m, *Solís 1531* (M). Guamate near Tambo, 3,020 m, *Solís 1532* (M). AZUAY: Vicinity of Cuenca, near union of the rivers Tarqui and Yanuncay, 2,700–2,900 m, *Camp 2637* (NY, RSA, US). PROVINCE UNKNOWN OR WITHOUT EXACT LOCALITY: Liusa, *Rose & Rose 23907* (US). Near Catocollas, *Mille 398* (US). Ecuador, *Weydahl in 1957* (S); *Bonpland 2011* (P); *Fraser in 1860* (G).

PERU. AMAZONAS: Chacapoyas, *Matthews* (NY). ANCASH: Baños de Chancos near Huaráz, ca. 2,950 m, *Sandeman 4617* (K). HUÁNUCO: Mito, 2,950 m, *Macbride & Featherstone 1528* (F, G, GH, S, US). LA LIBERTAD: Between Pampa and Yamobamba, ca. 70 km E of Trujillo, 3,050 m, *Conrad 2712* (MO). LIMA: Rimac, *Saratier 1397* (K). Lima, *Castelnau in 1847* (P); *Cuming 1079* (K). JUNÍN: El Mantaro near Jauja, *Ochoa 1000* (GH). Between Palca and Codapata near Tarma, 2,600–2,800 m, *Velarde 654* (RSA). WITHOUT EXACT LOCALITY: *Matthews in 1862* (NY); *Schweinitz* (K).

Oenothera laciniata can be distinguished from all other South American species of the genus by its nodding buds and also by the pitting of its seed coat (Fig. 191), characteristics that suggest a relationship with the North American *O. grandis* (Rose) Smyth (Fig. 194). If *O. laciniata* subsp. *pubescens* has indeed contributed a genome to both *O. nocturna* and *O. arequipensis*, one would think that there would be no barrier to hybridization between this entity and *O. featherstonei* and *O. verrucosa*, respectively. When *O. nocturna* was used as the female parent in crosses with *O. laciniata* subsp. *pubescens*, however, the F_1 hybrids were semiviable albinos that died after the production of only a few leaves. The reciprocal cross produced only empty seeds (Stubbe, pers. comm.), and the matter clearly needs further investigation.

46b. **Oenothera laciniata** subsp. **laciniata** Munz, N. Amer. Fl., ser. 2, 5: 109. 1965. [Synonymy not given.]

Plants with much less anthocyanin than in subsp. *pubescens*. Sepal tips 1–2 mm long, perhaps longer in North American specimens, erect to divergent. Sepals not flecked with red spots. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I).

Distribution: North American. Naturalized at one locality each in Paraguay, where it was collected once in cultivated ground in 1958, and in Brazil, where it was collected once in 1898.

Specimens examined:

BRAZIL. RIO GRANDE DO SUL: Pôrto Alegre, *Reineck in 1898* (LD).

PARAGUAY. SAN PEDRO: Alto Paraguay, primavera, cultivated, 1958, *Woolston 1024* (NY, S, SP, UC).

47. **Oenothera drummondii** Hooker, Bot. Mag. 61: *tab. 3361.* 1834; Munz, N. Amer. Fl., ser. 2, 5: 107. 1965. [Synonymy not given.]

Perennial herb, erect or ascending, forming a rosette, with a branched main stem and prostrate to arcuate-ascending side branches from the rosette, 2–6 dm tall. Plants densely gray-strigillose and very sparsely appressed to erect long-villous, also glandular-pubescent only on the sepals and floral tube. Rosette leaves narrowly oblanceolate, acute, gradually narrowed to the petiole, distantly sinuate-toothed, 6–18 cm long, 1–1.5 cm wide; cauline leaves narrowly elliptic to oblanceolate, acute, narrowly cuneate at the base, sessile or short-petiolate, remotely toothed, the teeth obtuse, to entire, rarely with large curved teeth near the base, 1.5–8 cm long, 0.5–2 cm wide; bracts narrowly elliptic, acute, narrowly cuneate at the base, sessile, remotely toothed, the teeth obtuse, to entire. Inflorescence branched. Flowers erect; young buds with a straight floral tube, the older ones with the floral tube curved upward. Floral tube 3–5 cm long. Buds lanceolate in outline, light green, 1.5–3 cm long, 0.5–1 cm thick; sepal tips 1–2 mm long, erect. Petals very broadly obovate, 2.5–5 cm long, yellow. Anthers 7–10 mm long. Filaments 12–21 mm long. Style 5–8 cm long. Stigma elevated above the anthers at anthesis; stigma lobes 4–8 mm long. Ovary 1–2.5 cm long. Capsule cylindrical, 3–5 cm long, 2–2.5 mm thick, arising from the stem at an angle. Seeds elliptic in outline, 1–1.5 mm long, 0.5–0.8 mm thick. Gametic chromosome number, $n = 7$ (7 bivalents or small rings at meiotic metaphase I).

Type: United States, Texas, Rio Brazos, *Thomas Drummond 26* (K, holotype; G, isotype).

Distribution: Texas to Veracruz, along the shores of the Gulf of Mexico; widely naturalized elsewhere, as near Supe in the vicinity of Lima, Peru, the only station known in South America.

Specimens examined:

PERU. LIMA: Prov. Chancay near Supe, in a wash near the beach at sea level, 1938, *Eyerdam 9067* (G, GH, K, MO, UC). Just N of Supe, in field near highway, sandy soil, not too dry, 1939, *Goodspeed 17362* (F, G, GH, K, MO, S, UC).

C. Subsect. EUOENOTHERA

Oenothera sect. **Oenothera** subsect. **Euoenothera** (Torr. & A. Gray) Dietrich, stat. nov. Based on *Oenothera* subg. *Euoenothera* Torr. & A. Gray, Fl. N.

Amer. 1: 492. LECTOTYPE: *Oenothera biennis* L.; Munz, N. Amer. Fl., ser. 2, 5: 120. 1965.

The description and full synonymy of this subsection will be given subsequently. It is entirely North American but widely naturalized throughout the temperate regions of the world.

48. **Oenothera erythrosepala** Borbás, Magyar Bot. Lapok 2: 245. 1903; Munz, N. Amer. Fl., ser. 2, 5: 130. 1965.

O. glazioviana Micheli in Martius, Fl. Bras. 13(2): 178. 1882. TYPE: Brasil, Rio de Janeiro, Tijuca, 7 Feb. 1868, *A. Glaziou 2568* (P, holotype, F-38382 photograph; BR, G, isotypes).
O. fusiformis Munz & Johnston, Contr. Gray Herb. 75: 21. 1925. TYPE: Ecuador, Prov. Loja, between El Tambo and La Toma, 1,000–2,200 m, 3 Sep. 1923, *A. S. Hitchcock 21350* (US-1196309, holotype; GH, NY, isotypes).
O. lamarckiana auct. mult., non Séringe in DC., Prodr. 3: 47. 1828.
O. grandiflora sensu Munz, Opera Bot., Ser. B, 3: 40. 1974, non L'Hér. ex Aiton, Hort. Kew. 2: 2. 1789.

Plants usually biennial, forming a rosette, erect, with simple or much-branched main stem and arcuate-ascending side branches from the rosette, 1–12 dm tall. Plants strigillose and coarsely erect-villous, some to many of the hairs with a red pustule at their base, the inflorescence mixed villous and glandular-pubescent. Rosette leaves narrowly lanceolate to oblanceolate, acute to subobtuse, gradually narrowed to the petiole, 13–30 cm long, 3–5 cm wide; cauline leaves narrowly elliptic to lanceolate, acute to almost obtuse, rather abruptly narrowed to the petiole, the uppermost sessile, 5–12 cm long, 2.5–4 cm wide; bracts lanceolate to narrowly ovate, acute, narrowly cuneate at the base, 1–3 (–5) cm long, 0.7–3.2 cm wide; all leaves undulate at the margins and sinuate-toothed to serrulate, sometimes reddish along the midrib. Inflorescence simple or branched. Floral tube 3.5–5 cm long. Buds lanceolate in outline, 3–4 cm long, 0.7–0.9 cm thick, often flushed with red. Sepals 2.8–4.2 cm long, 0.4–0.8 mm wide, red striped along the midrib; sepal tips 5–8 mm long, spreading. Petals very broadly obovate, retuse, 3.5–5 cm long. Anthers 10–12 mm long. Filaments 1.7–2.5 cm long. Style 5–8 cm long, the stigma held above the anthers at anthesis, its lobes 5–7 mm long. Ovary 0.7–1.2 cm long. Capsule narrowly lanceolate in outline, 2–3 cm long, 5–6 mm thick, green with a red median stripe on each valve, and with red-based bulbous hairs. Seeds prismatic, 1.3–2 mm long, 1–1.5 mm thick. Complex heterozygote but mostly outcrossing. Gametic chromosome number, $n = 7$ (ring of 12 and 1 bivalent at meiotic metaphase I).

Type locality: Hungary, Ráhos near Budapest.

Distribution: North America, Old World, but not known as a native plant anywhere and probably of European origin from introduced North American taxa; in South America cultivated and sometimes naturalized.

Specimens examined:

BRAZIL. MINAS GERAIS: Distr. Carangola, trail from Arapongo to Fazenda de Grama, 1930, *Mexia 4232* (F, GH, UC). RIO DE JANEIRO: Villa Theresa, 1876, *Glaziou 8343* (C, NY, P). Between Prata and Albuquerque near Nova Friburgo, 1,000 m, 1965, *Pabst & Sick 10746* (HB). SÃO PAULO: Ubatuba, 1895, *Loefgren 11700* (SP). City of São Paulo, cult. Jard. da Comissão, *Edwall in 1896* (POM, SP). Botanical Garden of São Paulo, 1902, *Loefgren 11898*

(SP). Cultivated in fields of the Instituto Agronômia, *Souza in 1944* (SP-52168). PARANÁ: Cultivated in the garden of the Facultad de Farmácia in Curitiba, 1966, *Moreira & Joly 373* (US).

URUGUAY. MONTEVIDEO: Miguelito, *Fruchard in 1874* (P). Montevideo, *Arechavaleta in 1902* (POM).

ARGENTINA. BUENOS AIRES: Mar del Plata, near Arroyo "Las Chacras," 1932, *Gelsii 114* (POM). Pergamino, 1932, *Parodi 9977* (POM). Cultivated in the Botanical Garden of the Facultad de Agronomía, 1939, *Munz 15455* (GH, POM). Mar del Plata, 1954, *Calderón 363* (BAA).

ECUADOR. Near Cotocollas, 1885, *Sodíro 333* (F, GH, NY, POM). LOJA: Catacocha, 2,050 m, 1946, *Enspinosa 622* (RSA).

PERU. ANCASH: Huaráz, 2,600–2,650 m, 1949, *Proaño 5142* (P).

CHILE. Jahuel, in *1902* (HBG). Coast of Chile, 1920, *Claude-Joseph 1251* pro parte (US).

Although the name *O. glazioviana* Micheli (1882) antedates *O. erythrosepala* Borbas (1903), and we believe that these names refer to the same entity, as indicated by the synonymy above, I am not making the substitution at the present time pending further studies of *Oenothera* subsect. *Euoenothera*, which I hope will clarify the taxa involved. The type of *O. glazioviana* might alternatively be equivalent to *O. suaveolens* Pers. (1805).

49. **Oenothera villosa** Thunb., Prodr. Fl. Cap. 75. 1794.

A more complete treatment of this North American species, being reported for the first time as a naturalized plant in South America, has been given by Munz (1965: 135–136); see Dietrich & Raven (1976) for a discussion of the name.

49a. **Oenothera villosa** subsp. **strigosa** (Rydb.) Dietrich & Raven, Ann. Missouri Bot. Gard. 62: 382. 1976.

Onagra strigosa Rydb., Mem. New York Bot. Gard. 1: 278. 1900.
Oenothera strigosa (Rydb.) Mack & Bush, Fl. Jackson Co. Missouri 139. 1902; Munz, N. Amer. Fl., ser. 2, 5: 135. 1965.

Biennial herb, forming a rosette, erect, with a simple or branched main stem and side branches that arise sharply from the rosette, 5–20 dm tall. Plants densely strigillose, with an admixture of villous and glandular pubescence on the floral tube and the sepals. Rosette leaves very narrowly elliptic to narrowly oblanceolate, gradually narrower toward the petiole, 10–20 cm long, 2–5 cm wide; cauline leaves very narrowly elliptic to narrowly elliptic, acute, narrowly cuneate at the base, short-petiolate to sessile, 7–15 cm long, 1–2.5 cm wide; bracts narrowly elliptic to lanceolate, acute, attenuate to cuneate at the base, sessile to short-petiolate, 1–5 cm long, 0.5–1.2 cm wide; all leaves plane to crinkled at the margins, shallowly sinuate-denticulate. Inflorescence simple or branched. Floral tube 2–3.3 cm long. Buds lanceolate in outline, 1–1.8 cm long, 0.4–0.6 cm thick. Sepals 11–15 mm long, 3–5 mm wide; sepal tips 1–3 mm long. Petals very broadly obovate, 0.8–1.7 cm long, yellow. Anthers 4–7 mm long. Filaments 8–15 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 3–4.5 cm long. Stigma lobes 3–5 mm long. Ovary 10–15 mm long. Capsule narrowly lanceolate in outline, spreading from the stem at an acute angle, 1.8–4.5 cm long, 4–6 mm thick. Seeds prismatic, 1.5–2 mm long, 1–1.5 mm thick, dark brown. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I).

Type: Locality unknown, Herb. Thunberg (S).

Distribution: Interior western United States and adjacent Canada. Naturalized at a few localities in the provinces of Córdoba, San Juan, and Mendoza, Argentina.

Specimens examined:

ARGENTINA. CÓRDOBA: Km 80 at Ruta 9, between Radio Nacional and Fabrica Postes de Cemento near Santa María, 1964, *Sublis 745* (CORD, MO). SAN JUAN: Calingasta, 1960, *Fabris & Marchionni 2391* (CTES, LP, M). Without definite locality, 1904, *Spegazzini 11274* (BAB). MENDOZA: Tupungato, 1933, *Ruiz Leal 1204* (Leal, POM). Dep. La Paz, Villa Pamonima, *Ruiz Leal in 1944* (Leal). Dep. Maipú, Las Barrancas, *Ruiz Leal in 1951* (Leal).

This species has not been reported previously from South America, although it is naturalized in several countries in Europe and in South Africa. The first collection from Argentina appears to be that of Spegazzini, cited above, made in 1904 in the province of San Juan; the species is apparently still not common. *Gaura parviflora* Dougl., another member of the Onagraceae from the Great Plains of North America, which resembles *O. villosa* in habit, is also present, apparently as an introduced plant, in Argentina, in the provinces of Córdoba and San Luis (Raven & Gregory, 1972). It was first collected in Argentina in 1876, and has spread to become much more common than *O. villosa*.

The widespread North American *Oenothera biennis* L., which is also abundantly naturalized in Europe, was collected once in a garden in Quilpué Prov. Valparaíso, Chile, by Lessauer in 1889 (M). It has apparently neither persisted nor spread, but it can easily be distinguished from *O. strigosa* by the lack of thick appressed strigulose pubescence, and more abundant glandular pubescence on the buds and in the inflorescence and its longer floral tubes (2.5 cm).

EXCLUDED AND DOUBTFUL NAMES

Oenothera australis Salisb., Prodr. Stirp. 278: 1796. No authentic material seen. Type locality: Argentina, prov. Santa Cruz, Puerto Deseado (Porte Desire). Probably *O. odorata* Jacq.

O. crispa Schultes, Obs. Bot. 73. 1809. No authentic material seen.

O. erosa Lehm., Linnaea 3(2): Litt. 8. 1828. No authentic material seen.

O. guttata Molina, Saggio Sul. St. Nat. Chile. ed. 2: 134. 1810. According to Reiche & Philippi, Fl. Chile 261. 1898 = *Mimulus guttatus* Fisch. ex DC.

O. malacophylla Spach, Nouv. Ann. Mus. Hist. Nat. 4: 344. 1835. No authentic material seen.

Onothera mandoni H. Lév., Monde Pl. 8. 109: As plate opposite p. 48. 1898; Monogr. Onoth. 359. 1909; Bull. Acad. Int. Géogr. Bot. 19: 319. 1909, nom. illeg.

Oenothera micans Tausch, Flora 22: 559. 1839. No authentic material seen.

O. polymorpha H. Lév. race *mollissima* (L.) H. Lév. var. *arechaveletae* H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909. No authentic material seen.

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